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Significance of Organic Detritus in the Diet of Larval Lampreys in the Great Lakes Basin

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Larval sea lamprey (*Petromyzon marinus*) and northern brook lamprey (*Ichthyomyzon fossor*) were collected monthly from three streams in the Upper Peninsula of Michigan from May 1992 through May 1993 and larval sea lampreys were collected during summer months from sites throughout the Great Lakes basin. Organic detritus made up most of the diet ash-free-dry-mass (AFDM) throughout the year, averaging 97.79%, with algae (2.12%) and bacteria (0.09%) making up the remainder of the diet AFDM. Assimilation efficiency for AFDM averaged 72% during warmer months and 53% during cooler months (annual mean = 61%). Gut fullness (amount of AFDM in the anterior one-tenth of the intestine) was low (mean = 0.10 mg diet AFDM·g^{-1} ammocoete). There were no significant differences in these measures between ammocoetes collected from the Upper Peninsula and those collected throughout the Great Lakes basin. From a laboratory-determined relationship between gut fullness and feeding rate, feeding rate in the field was estimated to be extremely slow, ranging from 4.2 to 5.5 mg diet AFDM·g^{-1} ammocoete·d^{-1}. These observations indicate that larval lampreys efficiently utilize a diet of organic detritus during warmer months when stream temperatures and food quality are more favorable for feeding, digestion, and growth.

Des larves de lamproie de mer (*Petromyzon marinus*) et de lamproie du nord (*Ichthyomyzon fossor*) ont été collectées mensuellement dans trois cours d'eau de la haute péninsule du Michigan de mai 1992 à mai 1993; des larves de lamproie de mer ont aussi été collectées durant les mois d'été dans des sites du bassin des Grands Lacs. Les détritus organiques représentatient la plus grande partie du poids sans cendre (PSC) des aliments au cours de l'année (moyenne de 97,79 %), les algues (2,12 %) et les bactéries (0,09 %) constituant le reste. L'efficacité de l'assimilation était en moyenne de 72 % pendant les mois les plus chauds et de 53 % pendant les mois les plus froids (moyenne annuelle de 61 %). La plénitude intestinale (PSC des aliments présents dans le dixième antérieur de l'intestin) était faible (moyenne = 0,10 mg de PSC des aliments par gramme d'ammocète). Il n'existait aucune différence appréciable quant à ces mesures entre les ammocètes collectés dans la haute péninsule et ceux qui provenaient du bassin des Grands Lacs. À partir d'un lien établi en laboratoire entre la plénitude intestinale et le taux d'alimentation, on a estimé que le taux d'alimentation était extrêmement lent (de 4,2 à 5,5 mg de PSC des aliments par gramme d'ammocètes par jour). Ces observations indiquent que les larves de lamproies utilisent efficacement leur alimentation en détritus organiques pendant les mois les plus chauds lorsque la température des cours d'eau et la qualité des aliments sont plus favorables à l'alimentation, à la digestion et à la croissance.

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Larval lampreys (ammocoetes) are suspension feeders that inhabit burrows in the soft sediment of streams. The larval phase may last from 3 to 13 yr. Their diet consists of a mixture of algae (primarily diatoms), organic detritus, and bacteria (Manion 1967; Moore and Beamish 1973). Although most investigators have focused their attention on the algal component (Creaser and Hann 1929; Schroll 1959; Manion 1967), algae actually comprise little of the diet. Based on indirect calculations, Moore and Potter (1976b) estimated that algae accounted for only 0.14 to 1.5% by volume of the diet of larval European brook lamprey (*Lampetra planeri*) in a eutrophic stream in England. They concluded that because algae contributed so little to the diet, ingested detritus and bacteria are probably more important to the nutrition of these animals.

Although organic detritus is frequently reported in the gut contents of all species of larval lampreys (Schroll 1959; Sterba 1962; Hardisty and Potter 1971), there are few estimates of its importance as a nutritional resource. A laboratory experiment by Moore and Potter (1976a) found that *L. planeri* ammocoetes increased in wet weight by 2.1% when fed 20–30 mg·L^{-1} detritus for 60 d at 15°C, but lost weight at this concentration over the same period at 5°C. Thus, the significance of organic detritus in ammocoete diets remains unclear.

The purpose of the present study was to directly quantify each dietary component (algae, bacteria, and detritus) and measure total diet assimilation over a thirteen month period for two species of larval lampreys to identify their principal nutritional resource. Feeding rate, estimated from gut fullness,

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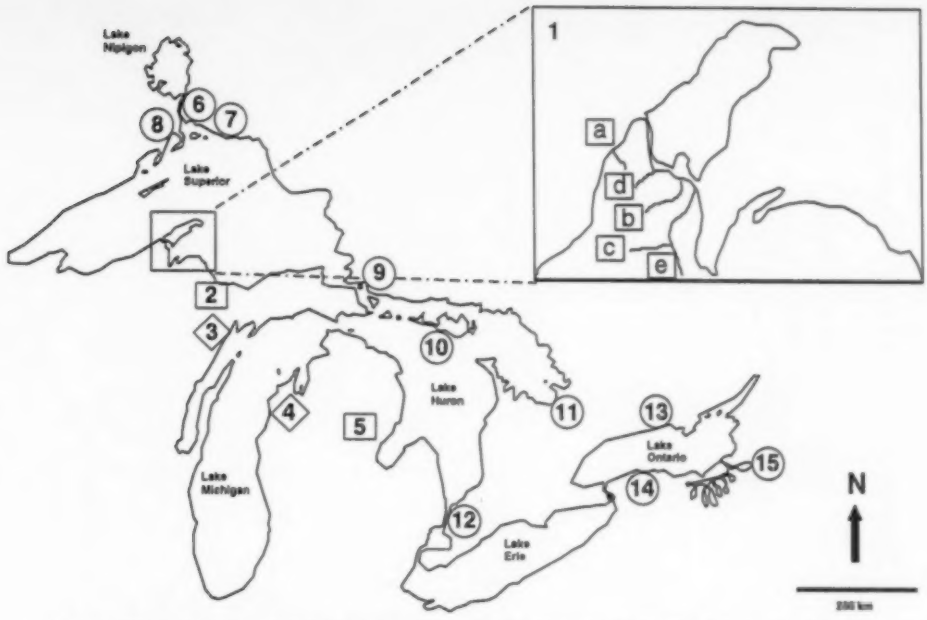

FIG. 1. River sites sampled for lamprey ammocoetes throughout the Great Lakes basin. Sites denoted with squares were sampled by Michigan Technological University, diamonds by the U.S. Fish and Wildlife Service, and circles by the Canadian Department of Fisheries and Oceans. Keweenaw sites are as follows: 1a-Misery River, 1b-Pike River, 1c-West Branch of the Sturgeon River, and 1d-Pilgrim River. For the remainder of site designations, see Table 1.

was also determined to further interpret the annual cycle of ammocoete feeding.

Methods

Sample Collection

Both sea lamprey (*Petromyzon marinus*) and northern brook lamprey (*Ichthyomyzon fossor*) ammocoetes were collected by electrofishing at monthly intervals from three streams in the Upper Peninsula of Michigan (hereafter termed Keweenaw sites) from May 1992 through May 1993 (Fig. 1; sites 1a, 1b, and 1c). Preliminary examination showed no differences in diet composition, assimilation efficiency, or gut fullness for samples collected at 4-h intervals over 24-h periods on two streams, so survey collections were made during morning hours for convenience. Due to prolonged flooding in all three streams as a result of ice and snow melt, ammocoetes were not sampled in April. At other sites throughout the Great Lakes basin, ammocoetes were obtained on single dates during the summer and fall of 1991 and 1992 by the U.S. Fish and Wildlife Service (Fig. 1; sites 3 and 4) and the Canadian Department of Fisheries and Oceans (Fig. 1; sites 1e-2 and 5-15).

Because ammocoetes are not responsive to electrofishing at temperatures <2°C (J. Weisser, U.S. Fish and Wildlife Service, Marquette, Mich., personal communication), diet samples during winter months (December–March) were obtained by placing lampreys in a cage in each stream. Cages were constructed of 1.27-cm plywood with outside dimensions: 0.3-m high × 0.6-m long × 0.45-m wide, providing a surface area of about 0.3-m^2. Openings in the front and back of the cages (0.3-m wide × 0.15-m high) were covered by 3-mm mesh netting that allowed flow through the cages but retained the lampreys. The cages were placed in areas of favorable ammocoete habitat and soft sediment was added to a depth of 0.15-m in each cage. Prior to introduction, ammocoetes were allowed to acclimate in the laboratory to ambient stream temperatures for two weeks. At monthly intervals, all ammocoetes were removed for analysis and replaced. As ammocoete density in each cage (ten per cage) was similar to densities observed in the field, no density-dependent cage effects should have occurred. This was confirmed in a field test conducted in May 1993, as diet composition, assimilation efficiency, and gut fullness of caged lampreys did not differ from those collected from streams by electrofishing (t-test; all $p > 0.25$).

For each sampling period and stream, ten freshly caught lampreys were held on ice until quiescent and anaesthetized with MS-222 (Sigma Chemical Corp.). This resulted in no loss of ingested material by regurgitation (Doxtater 1963). Lampreys were then fixed in 10% buffered formalin for 24 h and placed in Carosafe post-fixation preservative (Carolina Biological Supply) pending analysis.

Gut Content Analyses

The ammocoete digestive tract is a straight, undifferentiated tube approximately 45% of total body length (n = 305; SE = 0.01). Preliminary examination using yeast as a marker for detritus-fed ammocoetes indicated that there was no mixing or differential movement of diet contents. Thus, it can be assumed that ingested food material moves along the length of the intestine as plug flow. Contents were removed from the

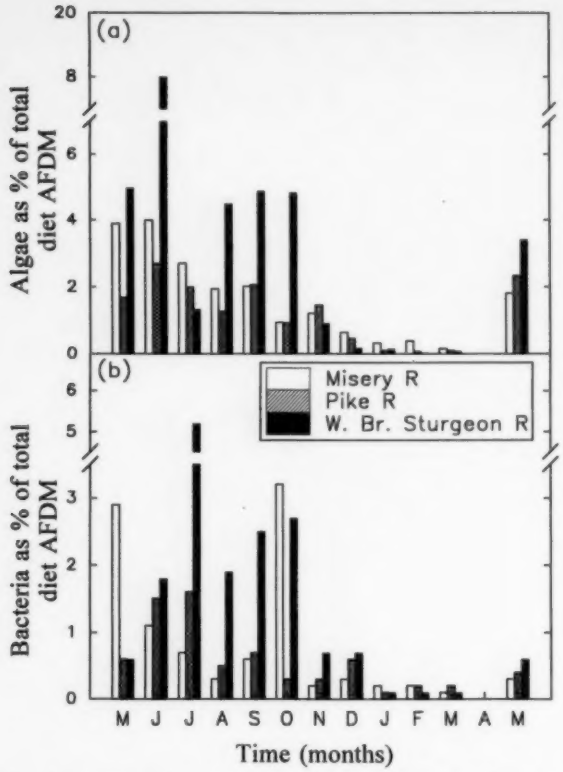

FIG. 2. Seasonal variation in the contribution of (a) algae and (b) bacteria ingested in ammocoete diets as a percentage of total diet AFDM for the Keweenaw sites from May 1992 through May 1993. Values for each month and stream are means of five individual ammocoetes.

anterior one-fourth of the intestine for five lampreys per sampling period per stream and a 50-μL subsample was analyzed by quantitative microscopy according to Ahlgren (1990a). Algal biovolume was estimated and converted to ash-free-dry-mass (AFDM) with an empirically determined weight/volume conversion factor (0.3633 mg AFDM·mm^{-3}) that is similar to ratios reported by Nalewajko (1966).

Contribution of bacteria to total diet AFDM was determined by staining a 50-μL subsample of the contents from the anterior one-fourth of the intestine with acridine orange (0.1 mg·mL^{-1} in 0.1 M potassium phosphate buffer, pH 7.5) according to Hobbie et al. (1977). Bacterial biomass per sample (mg AFDM·mL^{-1}) was calculated as [cells·mL^{-1}] × [mean biovolume (1 μm^3·cell^{-1}; vanDuyl and Kop 1990)] × [2.2 × 10^{-10} mg C·μm^{-3}; carbon conversion factor of Bratback and Dundas 1984] × [0.5 AFDM·mg C^{-1}].

The remainder of the sample was dried to constant weight at 110°C and total sample AFDM was calculated as weight loss after combustion at 550°C. The AFDM of organic detritus was calculated indirectly as total AFDM minus microorganism AFDM (Bowen 1979a).

Assimilation Efficiency

Assimilation efficiency (%AE), the net amount of food assimilated through the gut wall expressed as a percentage of the amount ingested, was determined for total organic matter as described by Conover (1966). AFDM in gut contents taken separately from the first and last tenths of the digestive tract were compared, using diet ash as an unassimilated reference material. The assumption that ash is not assimilated is reasonable inasmuch as most of the ash appears to be small sand grains and diatom frustules. To the extent that this assumption is incorrect, assimilation efficiency will be underestimated. Because there was not enough food in the first and last tenth of the intestine to calculate individual assimilation efficiencies, gut contents of five lampreys per sampling period per stream were pooled for this analysis.

Feeding Rate

Gut fullness

As an index of feeding rate, fullness of the anterior one-tenth of the intestine was measured for ammocoetes caught in the field as mg diet AFDM·g^{-1} ammocoete wet weight. The same five lampreys per sampling period per stream used in determining assimilation efficiency were used to estimate gut fullness.

Laboratory feeding experiment

Sea lamprey ammocoetes were obtained from the Hammond Bay Biological Station (U.S. Fish and Wildlife Service), Millersburg, Mich., in December 1992 and were acclimated to laboratory conditions for 3 wk on a diet of stream detritus.

Detritus was collected from an area in the Pilgrim River known to support ammocoetes. The upper 2.5 cm of sediment were removed using a plastic scoop, sieved, and the fraction >45-μm allowed to settle for 10 min. Suspended detritus was poured off and fed to 36 groups of three ammocoetes (average 3.21 ± 0.64 g live weight per aquaria; 0.21–0.32 g·L^{-1}). Ammocoetes were held in aerated, glass aquaria with 12 L of conditioned water. Each aquarium contained sieved sand (<1 mm) to a depth of 7.5 cm and photoperiod was maintained on a 12 h L:12 h D cycle. To control temperature, twelve glass aquaria were held in each of three Living Stream refrigerated tanks with constant water circulation (Frigid Units Inc.). Experiments were conducted at 2, 9, and 16°C, simulating average winter, spring/fall, and summer temperatures, respectively, in Upper Peninsula streams.

To measure feeding rate, Red 40 Alum Lake (a water insoluble, particulate food dye; Warner-Jenkinson Inc.) was used as a visible tracer. Preliminary experiments showed that a concentration of 100 mg·L^{-1} of the dye was needed to allow detection in ammocoete guts. This concentration appeared not to disturb the normal feeding behavior of ammocoetes. Because ammocoetes normally feed on particles at much lower concentrations (<40 mg·L^{-1}), it appears that their feeding mechanism has a low capture efficiency for these dye particles. Detritus was added to the aquaria at a concentration of 30 mg·L^{-1}, as this is comparable to that found suspended in depositional areas in many natural waterways (Moore and Potter 1976a).

The detritus/dye mixture was added to each aquarium and ammocoetes were allowed to feed for several hours before being removed and sacrificed. Each digestive tract was removed and preserved in 10% buffered formalin and the distance the detritus/dye mixture traveled was measured to the nearest millimetre. Contents were removed, dried to

TABLE 1. Means (SE) for percent AFDM in the diet, percent contribution of algae and detritus to diet AFDM, assimilation efficiency of AFDM, and gut fullness of AFDM for sea lamprey ammocoetes sampled throughout the Great Lakes basin.

Site No. (Fig. 1)	Stream	Date	AFDM	Algae	Detritus	Assimilation efficiency	Gut fullness
8	Black Sturgeon R	08-13-92	54.42 (3.72)	0.64 (0.16)	99.36 (0.16)	86.44	0.31 (0.06)
2	Chocolay R	09-06-91	61.76 (5.19)	2.15 (0.38)	97.85 (0.38)	—	—
2	Chocolay R	09-12-91	44.20 (9.96)	7.83 (1.07)	92.24 (1.05)	—	—
15	Fish Cr	09-17-92	65.32 (6.93)	0.81 (0.10)	99.19 (0.10)	63.57	0.44 (0.08)
7	Gravel R–Mtn Bay	08-15-92	58.94 (7.38)	0.44 (0.22)	99.56 (0.10)	78.63	0.18 (0.05)
6	Nipigon R–Lake Helen	08-28-92	63.83 (10.63)	0.91 (0.31)	99.09 (0.31)	69.05	0.19 (0.04)
11	Nottawasaga R	09-09-92	68.04 (1.29)	1.90 (0.57)	98.10 (0.57)	49.06	0.34 (0.06)
4	Platte R	03-23-92	85.20 (4.91)	0.82 (0.07)	99.18 (0.07)	66.44	—
4	Platte R	04-29-92	62.35 (7.61)	2.87 (0.34)	97.13 (0.34)	77.92	—
4	Platte R	06-23-92	62.23 (3.40)	1.49 (0.23)	98.51 (0.23)	76.26	0.14 (0.01)
3	Rapid R	10-24-91	73.83 (7.34)	1.66 (0.59)	98.34 (0.59)	—	—
5	Rifle R	07-21-92	57.66 (6.59)	4.23 (1.27)	95.77 (1.27)	79.11	—
13	Salem Cr	09-19-92	74.43 (5.57)	1.80 (0.45)	98.20 (0.45)	62.33	0.27 (0.03)
14	Salmon Cr	09-11-92	59.93 (6.00)	1.97 (0.72)	98.03 (0.72)	70.69	0.41 (0.12)
12	St. Clair R	07-27-92	61.39 (7.29)	1.13 (0.46)	98.79 (0.54)	81.36	0.37 (0.10)
9	St. Marys R	08-27-92	76.61 (3.61)	0.20 (0.07)	99.80 (0.07)	85.58	0.21 (0.14)
1e	Sturgeon R	08-20-91	46.72 (9.44)	2.49 (0.55)	97.52 (0.54)	—	—
1e	Sturgeon R	08-31-91	44.35 (5.16)	5.53 (1.74)	94.50 (1.75)	—	—
10	Timber Bay Cr	07-07-92	39.77 (7.04)	0.53 (0.12)	99.47 (0.12)	56.93	0.10 (0.01)
	Mean		61.10 (6.26)	1.98 (0.43)	98.03 (0.43)	71.67 (2.95)	0.25 (0.04)

constant weight at 110°C, combusted at 550°C, and reweighed. Gut fullness and feeding rate were measured as mg diet AFDM in the anterior one-tenth of the intestine·g^{-1} ammocoete wet weight, and mg diet AFDM ingested·g^{-1} ammocoete wet weight·h^{-1}, respectively.

Results

Diet Composition

Throughout the Great Lakes basin, for all sites and months sampled, organic detritus made up most of the diet, averaging 97.79% of total diet AFDM. Algae contributed 2.12%, with diatoms alone comprising 1.79%. Bacteria were limited to 0.09% (data collected for Keweenaw sites only) of the total diet AFDM. Diets of sea lamprey and northern brook lamprey ammocoetes were made up of algae, bacteria, and detritus in proportions that were not significantly different (ANOVA; all $p > 0.25$).

Algal and bacterial abundance in streams sampled at monthly intervals at the Keweenaw sites from May 1992 through May 1993 followed distinct seasonal patterns. As a percentage of diet AFDM, algal abundance peaked in May/June and September for all three sites (two-factor ANOVA; both $p < 0.001$; Fig. 2a). The cycle of bacterial abundance lagged about one month behind algal abundance, with peaks in July and October (two-factor ANOVA; both $p > 0.25$; Fig. 2b). Abundance of algae and bacteria in the diet declined in all three streams from November through March (Fig. 2). Winter samples (November–March) contained a significantly lower algal and bacterial biomass than samples collected during warmer periods (May–October) in all three streams (t-test; all $p < 0.001$). Algal and bacterial abundance in the diet, as a percentage of total AFDM, increased in May following the spring thaw as streams resumed more typical flows, temperatures warmed, and light levels increased (Fig. 2).

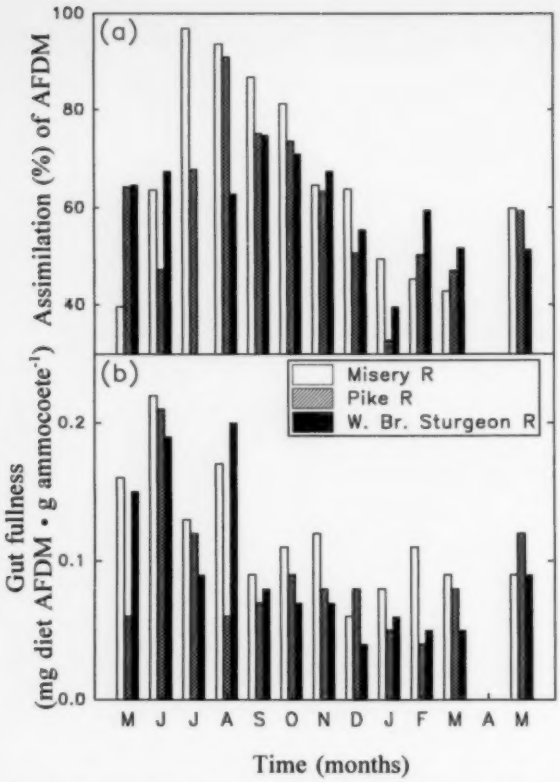

FIG. 3. Seasonal variation in the (a) assimilation and (b) gut fullness of organic matter ingested by ammocoetes for the Keweenaw sites from May 1992 through May 1993. Estimates for each month and stream consist of five pooled ammocoetes for assimilation efficiency and means of five individual ammocoetes for gut fullness.

From May through October 1992, the amount of algal AFDM in the diet was higher, on average, in the West Branch of the Sturgeon River (6.46%), which has a canopy that remains relatively open, than in either the Misery (2.57%) or Pike (1.77%) rivers, which have closed canopies (ANOVA; $p < 0.001$). An unusually large spate in the Sturgeon River in July appears to have swept away much of the algae, resulting in a lower algal abundance in the diet for that month relative to all other summer months in that stream (ANOVA; $p < 0.01$; Fig. 2a).

Ammocoetes sampled from the remainder of the Great Lakes basin showed similar diet composition to ammocoetes sampled at Keweenaw sites (ANOVA; $0.15 < p < 0.20$; Table 1). Riparian canopy was categorized as open or closed by field personnel of the Canadian Department of Fisheries and Oceans Sea Lamprey Control Centre. The amount of algal AFDM in the diet was typically higher for streams with open canopies (Fig. 1; sites 1d, 2, 3, 4, 5; Table 1). Algal abundance in open canopy streams was, on average, 3.98% of total diet AFDM, whereas closed canopy streams had an algal abundance averaging only 1.27% (t-test; $p < 0.02$). Four deep-water sites were unshaded by riparian vegetation but ammocoetes collected from these contained little algae. Two were lentic environments (Fig. 1; sites 6 and 7) and

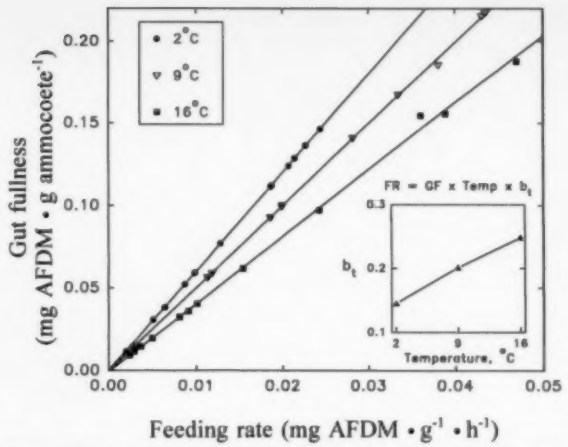

FIG. 4. Relationship between feeding rate and gut fullness at 2, 9, and 16°C as determined from the laboratory feeding experiment.

two were in large rivers (Fig. 1; sites 9 and 12). Both habitat types have low light penetration to bottom substrate which impedes the development of algae. However, a suitable environment exists for ammocoetes (Wagner and Stauffer 1962).

Assimilation Efficiency

In July 1992, we determined assimilation efficiencies for nine large individual northern brook lamprey ammocoetes (range 120–155 mm TL) from the Pike River. Mean %AE was 78.08% with a relatively low level of variation (range 71.01–84.38%; CV = 5.92%). More typically, ammocoetes collected were too small (60–90 mm TL) to provide adequate gut samples to determine individual %AE. As there was little variation between ammocoetes collected at the same time within a stream, we pooled samples from five individuals for monthly measures of %AE.

Throughout the year, lamprey ammocoetes assimilated, on average, 61% of organic detritus ingested. For the Keweenaw sites, %AE followed a seasonal cycle, peaking in July or August (Fig. 3a). Percent AE was higher during warmer months (May–October; mean = 72%) than during colder sampling periods (November–March; mean = 53%) (t-test; $p < 0.05$). Flooding in the West Branch of the Sturgeon River in July caused a change in diet composition resulting in no assimilation of ingested material (Fig. 3a). Assimilation efficiency estimates from the remainder of Great Lakes basin sites (Table 1) fall within the range of values for ammocoetes sampled during late summer at the Keweenaw sites (Fig. 3a).

Feeding Rate

For the Keweenaw sites, gut fullness followed a seasonal cycle, peaking in June and decreasing through the remainder of the year (Fig. 3b). During warmer months (May–October), gut fullness was higher (0.13 mg diet AFDM·g^{-1} ammocoete wet weight) than in colder sampling periods (November–March; 0.07 mg diet AFDM·g^{-1} ammocoete wet weight) (t-test; $p < 0.02$; Fig. 3b). Ammocoetes sampled from the remainder of Great Lakes basin sites typically had gut fullness values (Table 1) within the range found for ammocoetes sampled at the Keweenaw sites during late summer (Fig. 3b).

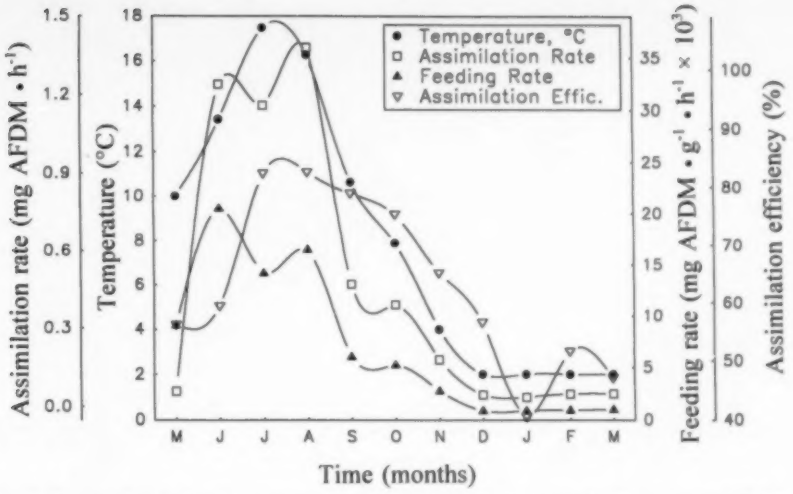
Temperature, °C
Assimilation Rate
Feeding Rate
Assimilation Effic.
Assimilation rate (mg AFDM • h⁻¹)
Temperature (°C)
Feeding rate (mg AFDM • g⁻¹ • h⁻¹ × 10³)
Assimilation efficiency (%)
M J J A S O N D J F M
Time (months)

FIG. 5. Seasonal variation in stream temperature, assimilation rate, feeding rate, and %AE as estimated for the Keweenaw sites.

In the laboratory feeding experiment, mean feeding rates were 1.43×10^{-2}, 3.67×10^{-2}, and 3.21×10^{-2} mg diet AFDM·g^{-1} ammocoete wet weight·h^{-1} at 2, 9, and 16°C, respectively. Gut fullness values at these temperatures were 0.08, 0.11, and 0.07 mg diet AFDM·g^{-1} ammocoete wet weight. Although within-treatment variance was relatively high (CV = 58.51%), regression slopes of feeding rate and gut fullness between temperature treatments were significantly different (ANCOVA; both $p < 0.001$).

From field gut fullness estimates and the experimentally determined slope of the regression relationship between gut fullness and feeding rate (b_i; Fig. 4), we calculated feeding and assimilation rates for wild populations of lamprey ammocoetes from the Keweenaw sites for the period May 1992 through March 1993. Feeding rate (FR) was estimated as the product of gut fullness (GF), stream temperature (Temp), and the slope (b_1) (Fig. 4). Assimilation rate (AR) was estimated as the product of feeding rate (FR) and field determined %AE.

Discussion

Seasonal Variation in the Abundance of Algae and Bacteria

Variation in the abundance of algae in ammocoete diets follows the general annual cycle described for north temperate streams (Hynes 1970). Algae in diets peaked in late spring and early autumn when light availability and stream temperatures support high levels of diatom production (Chapman and Demory 1963; Hynes 1970). A similar cycle of algal abundance in ammocoete diets has also been reported in other studies (Moore 1972; Moore and Beamish 1973; Moore and Mallatt 1980). Bacterial abundance in the diet also followed a seasonal cycle, lagging about a month behind peaks in algal abundance. This may reflect the time required for bacterial population growth that is fueled by organic substrates from physiologically mature or senescent algae. Thus, variation in the abundance of algae and bacteria in ammocoete diets is consistent with the expected pattern of their availability in the annual stream cycle.

Sources of Nutrients Supporting Lamprey Larvae

Organic detritus is the principal trophic resource supporting the metabolism and growth of both sea lamprey and northern brook lamprey larvae in the populations studied. Microorganisms averaged only 2.2% of diet AFDM. Even if these are digested with 100% efficiency, their low concentration means they could account for no more than 4% of the organic matter assimilated. Because detritus makes up an average of 98% of diet AFDM and diet AFDM is assimilated with a mean efficiency of 61%, it is necessarily the case that most organic matter assimilated is detritus. The same conclusion was reported for two teleosts, *Oreochromis* (*Sarotherodon*) *mossambicus* (Bowen 1981) and *Prochilodus lineatus* (*platensis*) (Bowen et al. 1984), that feed on similar mixtures of aggregated detritus and microorganisms.

Although microorganisms provide a small fraction of the digesta, they may be important as sources of specific nutrients, especially vitamins, or as supplementary sources of digestive enzymes. Of much greater significance, they may play a critical role in production of the detrital fraction of the diet. There is a strong correlation between microorganism abundance and the digestibility of detritus, with assimilation efficiency lagging about one month behind microorganism abundance. Algal and bacterial abundances in ammocoete diets peaked in June and July, respectively, whereas peak %AE occurred in July and August. After October, %AE and microorganism abundance declined as stream temperatures cooled. Percent AE reached a low in January, increasing slightly in February before declining again in March (Fig. 3a). This February increase coincided with a period of warmer air temperatures from mid-January to early February 1993 that caused some stream ice melt, allowing light penetration to the stream bottom in some reaches for approximately two weeks.

The correlation in the annual cycles of microorganism abundance and assimilation efficiency points to algae and bacteria as agents responsible for the production of more digestible detrital aggregate. At the Keweenaw sites, the four- to six-week-long period of high discharge following spring snow melt either buries or scours from the system

much of the algae, bacteria, and organic detritus. This is followed in May and June by a spring diatom bloom during which cells begin to lay down layer upon layer of extracellular polymer matrix. Production of extracellular matrix is greater after the stationary growth phase as diatom cells become more physiologically mature (Decho 1990). This material entraps existing particles, adsorbs dissolved organic matter (DOM) and gradually builds up a "biofilm" layer (Decho 1990) comprised of "detrital aggregate" (Bowen 1979b). We speculate that the lag between peaks in diatom abundance and detritus digestibility (%AE) reflects the time required for detrital aggregate to accumulate, be dislodged by physical erosion, sloughing (Decho 1990), and invertebrate activity (Allanson 1973), and become a significant component of suspended particulate organic matter (POM) in streams. These newly produced particles are likely to be less degraded and refractory, and to have a higher food value than older particulate matter, especially that derived from vascular plant debris (Bowen 1979b). Not only do biofilms potentially represent a highly labile carbon source because they are more abundant in easily hydrolyzable polysaccharides, but the DOM adsorbed to their surface provides a reservoir of nutrients and organic compounds that are otherwise not available to particulate feeding organisms (Decho and Lopez 1993). Thus, we believe that the peak in %AE is likely due to increased availability of recently produced, more digestible detrital aggregate relative to other sources of detrital particles in streams. The correlation between bacterial abundance and the digestibility of detrital aggregate for lamprey larvae suggests that both heterotrophs derive their nutrition from labile detrital aggregate.

This interpretation of the annual cycle is consistent with the effects of the July flood in the West Branch of the Sturgeon River. Flood waters appear to have swept away both algae and detritus, leaving only indigestible sediment in suspension for ammocoete feeding. This heavy bedload movement resulted in ammmocoete diets containing an extremely high percentage of mineral matter compared with other months of the year. Typically, ammocoete diets contained, on average, 35% mineral matter (range 14.80–61.25%; SE = 2.06). However, in July, ammocoete diets contained 75% mineral matter. After stream discharge returned to normal, algal abundance increased in August and diet digestibility peaked later in September. Thereafter, the pattern for the Sturgeon River was comparable to the other two streams.

Seasonal Variation in Gut Fullness and Feeding Rate

Gut fullness and feeding rate appear more closely associated with stream temperature than with diet digestibility. An increase in stream temperature up to 15°C in early summer was associated with an increase in gut fullness, feeding rate, %AE, and assimilation rate (Fig. 5). Peak stream temperatures in July coincided with a decrease in feeding and assimilation rate, but a peak in %AE. Reduced feeding at this time may have been a response to the increased availability of digestible detrital aggregate, allowing the larvae to meet their nutritional needs while ingesting a smaller quantity of food. As stream temperature declined after the peak, feeding and assimilation rates increased again before declining through the remainder of the year (Fig. 5). This pattern points to the annual temperature cycle as a major influence on ammocoete feeding in north temperate streams (R^2 = 0.60 and 0.57 for %AE and gut fullness, respectively; both $p < 0.001$). Malmqvist and Brönmark (1981) reported a similar response, in that stream water temperature has a significant effect on the rate of particle filtration in *L. planeri* ammocoetes. However, the availability of a higher quality food source in biofilm detritus during the summer makes it difficult to separate the relative contribution of both temperature and food quality on ammocoete feeding.

Ammocoete Adaptations to Detritivory

Compared with other detritivorous fishes, the digestive tract of lamprey ammocoetes is unspecialized (Hardisty and Potter 1971). It consists of little more than a simple tube about half as long as the animal's body, with some differentiation into esophagus and intestine. As no mucosal folds or lateral caeca are evident, the surface area for absorption appears to be small. Also, the pH in the intestine of ammocoetes is circumneutral, typically around 7.5 (Barrington 1972). Other detritivorous fishes studied to date show morphological adaptations for digestion of detritus (Bowen 1980, 1984; Mundahl and Wissing 1988). Yet lamprey ammocoetes assimilate an average of 61% of the organic matter in their diets, a percentage similar to that reported for other detritivorous fishes (Bowen 1981; Bowen et al. 1984; Mundahl and Wissing 1988; Ahlgren 1990b). The question remains, how can lamprey ammocoetes so efficiently utilize a low quality food resource such as detritus while having no apparent morphological adaptations of their digestive tract?

Ammocoetes feed very slowly. We estimate from gut fullness data and the experimentally determined gut fullness/feeding rate relationship that at between 9 and 15°C, ammocoetes feed at rates ranging from 4.2 to 5.5 mg diet AFDM·g^{-1} ammocoete·d^{-1}. This is far below the 60 mg diet AFDM·g^{-1} fish·d^{-1} typical of other juvenile fishes fed highly digestible diets *ad libitum* (Brett and Groves 1979, *inter alia*). Slow feeding is consistent with observations that ammocoetes' respiratory pumping rate and metabolic rate are both slower than those observed for other fishes (Mallatt 1982; Sterba 1962; Hill and Potter 1970) and with the long time period required for gut clearance in ammocoetes (Moore and Mallatt 1980). In the absence of discernable morphological adaptations for digestion of detritus, it appears that ammocoetes achieve a high assimilation efficiency with an extraordinarily long period of digestion. This suggests that natural selection may have favored a low metabolic rate as an adjustment to the limited nutrient assimilation rate associated with this digestive strategy. In turn, low metabolism is linked to slow growth and the extended length of the detritivorous larval phase (3–13 yr; Applegate 1950; Lowe et al. 1973). Thus, many of the life history characteristics of lamprey larvae can be interpreted as adaptations to organic detritus as a food resource.

The destructive impact of sea lamprey predation on Great Lakes fishes is currently partially controlled by chemical treatment of streams to kill larvae before most metamorphose into the parasitic form. Due to both cost and limited effectiveness, the level of control in many parts of the basin is not adequate to support management objectives. There is a growing need to supplement or replace the current control technology with less expensive, more effective, and more environmentally benign technologies. Identification of the link between the detritus food resource and larval

lamprey production may provide a step toward identifying opportunities for new control strategies.

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Bioaccumulation of Radiocesium by Fish: the Influence of Physicochemical Factors and Trophic Structure

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Although many measurements have been made on radiocesium levels in water and aquatic biota, no agreement has been reached regarding the factors affecting bioaccumulation of these radionuclides. With monitoring data from countries that operate nuclear facilities and data from the primary literature, we explored the chemical and ecological factors that determine the bioaccumulation of radiocesium. Using log–linear regression we found that the bioaccumulation of ^{137}Cs by fish was a negative function of both dissolved potassium and suspended sediment concentration, and a positive function of temperature. Important ecological factors were the trophic level of the fish (piscivores bioaccumulate more than planktivores and benthivores), and the length of the food chain as reflected by the ratio of piscivore yield relative to net primary production. Fish from softwater drainages, which make up a large portion of northern Europe and Canada, are more vulnerable to radiocesium contamination than fish from hardwater sedimentary drainages, because these waters are extremely low in potassium and suspended sediment, and their watersheds are less efficient in retaining radiocesium. High dissolved potassium, short food chains, and the much greater volume and mixing potential of the ocean make marine fish less vulnerable to releases of radiocesium.

Bien que l'on ait effectué du nombreux dosages des concentrations de césium radioactif dans l'eau et les biotes aquatiques, on ne s'entend pas sur les facteurs en cause dans la bioaccumulation de ces radionucléides. À l'aide de données de surveillance provenant de pays qui exploitent des installations nucléaires et de données fondamentales, nous avons examiné les facteurs d'ordre chimique et écologique qui déterminent la bioaccumulation du césium radioactif. Au moyen d'une régression log–linéaire, nous avons montré que la bioaccumulation de ^{137}Cs par les poissons était une fonction négative des concentrations de potassium dissous et des sédiments en suspension et qu'elle était une fonction positive de la température. Des facteurs écologiques importants étaient le niveau trophique des poissons (la bioaccumulation est plus importante chez les piscivores que chez les planctivores et les benthivores) et la longueur de la chaîne alimentaire établie par le rapport entre le rendement des piscivores et la production primaire nette. Les poissons des eaux douces de ruissellement, qui constituent une grande partie du nord de l'Europe et du Canada, sont plus susceptibles à la contamination par le césium radioactif que les poissons des eaux dures sédimentaires de ruissellement, puisque ces eaux ont des teneurs extrêmement faibles en potassium et en sédiments en suspension et que leurs bassins versants retiennent moins efficacement le césium radioactif. La concentration élevée de potassium dissous, les courtes chaînes alimentaires ainsi que le volume et le potentiel de mélange beaucoup plus considérables des océans rendent les poissons marins moins susceptibles aux rejets de césium radioactif.

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Radiocesium isotopes are abundant fission products that decay slowly (^{137}Cs and ^{134}Cs have half-lives of 30.17 years and 2.07 years, respectively) and accumulate in biota by virtue of their high assimilation and slow clearance from living tissue (Kolehmainen 1972; Ugedal et al. 1992). Interest in these radionuclides dates back to the 1950s when aboveground nuclear weapon tests resulted in contamination of the stratosphere. Atmospheric weapon tests along with the operation of nuclear facilities such as generating stations, fuel reprocessing plants, and waste disposal areas have led to continual releases of these contaminants to the environment. The combined effect of these emissions has resulted in both point source and global pollution. Recently, the nuclear accident at Chernobyl has renewed interest in these cesium (Cs) radioisotopes (e.g., Hakanson et al. 1992; Elliott et al. 1992). Although many measurements have been made on radiocesium levels in water and in virtually any type of aquatic biota, no agreement seems to have been reached regarding the factors that affect the bioaccumulation of these radionuclides, and this lack of ecological understanding has hindered the development of robust dose models.

The fate and cycling of radioactive isotopes in ecosystems has long been a subject of vital interest to applied

ecologists and health physicists (Davis and Foster 1958; Krumholz 1956); however, it is also of fundamental significance in biogeochemistry and trophodynamics (Hutchinson and Bowen 1950; Rigler 1956; King 1964; Marples 1966; Odum 1965). Although Cs is itself not biologically essential, the pathways that cycle this element within the ecosystem, and the processes that lead to its bioconcentration are the fundamental physiological and energetic pathways and processes that dominate ecosystem function.

While some authors have emphasized the role of dissolved cations as nonisotopic carriers (especially potassium) in reducing biouptake of radiocesium (Williams and Swanson 1958; Davis 1963; Kolehmainen et al. 1967; Preston et al. 1967), others have denied these effects (Mailhot et al. 1988). Food chain factors are equally problematic. While there is general agreement that food is the major route of radiocesium uptake by fish, some authors claim varying degrees of biomagnification (Gustafson 1967; Eyman and Kevern 1975; Hammar et al. 1991), some deny food-chain effects (Nelson 1969; Reichle et al. 1970; Kolehmainen 1972; Thomann 1981), and some even claim that radiocesium undergoes "biodiminution" in aquatic food chains (Mailhot et al. 1988). Clearly both the biochemical and ecological aspects of radiocesium biouptake remain shrouded in controversy.

Although the problem of radiocesium bioaccumulation is of major ecological and radiological importance, its analysis is impeded by the fact that most of the monitoring data have been collected for the purpose of calculating site-specific doses to be used by local regulatory agencies, and have not been published in the primary scientific literature. The relative inaccessibility of most of this "gray" government and industrial literature has prevented a thorough review of the subject, and those reviews that have been attempted have used only a fraction of the data that have been collected by monitoring agencies (Reichle et al. 1970; Vanderploeg et al. 1975; Blaylock 1982; Mailhot et al. 1988). The purpose of this study was to collect as much of the monitoring data as possible from countries that operate nuclear facilities, to combine these with the information available in the primary literature, and, using statistics, to explore the chemical and ecological factors that determine the bioaccumulation of radiocesium. The empirical models generated in this analysis can be used to evaluate the potential contribution to risk associated with the consumption of fish from sites near nuclear reactors. Although most of the radiocesium monitoring data that we have compiled in this study come from sites near nuclear power stations, there are sufficient data available from remote sites in Canada to permit a comparison with sites near nuclear stations. These remote sites include Lake Superior, the Ottawa River, and the three basins of Great Slave Lake.

Hypotheses

Besides collecting data on radiocesium concentrations in fish and their bioaccumulation factor (relative to water), we compiled data on a number of physicochemical and ecological factors that we hypothesized to be important determinants of the partitioning of radiocesium between water and biota.

The first hypothesis that we test can be termed the "potassium carrier" hypothesis; we expect to see a reduction in the radiocesium bioaccumulation factor with increasing potassium (K) concentration of the water. Although the primary route of radiocesium and K uptake in fish is through food, and food varies little in its K content, we expect to see this inverse relationship, because the major route of radiocesium entry into the food chain is through direct absorption by plants from water. Plants absorb cations through an active transport mechanism that clears H^+ ions from the cell, making the cell interior negative, and resulting in indiscriminate uptake of cations with radii small enough to pass through membrane channels. Thus, rubidium and Cs enter the plant cell along with the more abundant and essential K ions (MacRobbie 1974; Kochlan and Lucas 1982). While the flux of ions into the cell increases with the external concentration (Kochlan and Lucas 1982) the flux relative to the external concentration decreases, and thus the uptake of K (and therefore radiocesium) relative to its external concentration will diminish with increasing K concentration. Thus, algal cells bioaccumulate radiocesium about two to three orders of magnitude when K is about 10 μM, and by only about one order of magnitude when K is about 10 mM (Williams and Swanson 1958; Williams 1960). Thus, most of the radiocesium bioaccumulation in the food chain occurs at the primary producer level; therefore, we expect the K dilution effect seen in plants to be manifested in fish at all trophic levels.

As radiocesium is known to be efficiently assimilated (Kolehmainen 1972; Forseth et al. 1992) and cleared very slowly by fish (biological half-life in the hundreds of days; Kolehmainen 1972; Ugedal et al. 1992), most theoretical models presume that radiocesium will be biomagnified to some degree by aquatic food chains (Forseth et al. 1991). This has been well documented for a wide variety of persistent environmental contaminants with long biological half-lives such as organochlorines (Thomann 1981; Rasmussen et al. 1990; Borgmann and Whittle 1992; Rowan and Rasmussen 1992) and mercury (Borgmann and Whittle 1992; Cabana et al. 1994). Although we expect to find significantly higher radiocesium levels in piscivorous fish than in planktivorous or benthivorous fish, the effect has never been rigorously quantified by empirical analyses.

Uncharacteristically high or low bioaccumulation factors have been estimated for fish in Scandinavia in the few years following the pulse release of radiocesium from Chernobyl in 1986 (Sundblad et al. 1991). This results from the time lag associated with the clearance of a pulse through long food chains, and underscores the need to concentrate on equilibrated systems, when attempting to estimate bioaccumulation factors empirically. We have excluded from our analysis data collected in Europe after 1986, as the detailed time series required to integrate across the pulse for each fish species over time were not available. While we have restricted our analysis to "quasi-equilibrated" sites, pulses are to some extent inevitable because releases from weapon tests and from nuclear facilities change from year to year. Fish low in the food chain would tend to track such variations closely, and thus we should expect to see linear relationships (log–log slopes near 1) between planktivore radiocesium levels and levels in water (bioaccumulation of the isotope in fish relative to water (BAF) independent of water concentrations). Piscivores, on the other hand, are not likely to track variations as closely, and thus we would expect to see log–log slopes <1; that is BAFs estimated at high water concentrations might be somewhat lower than those estimated

at low water concentrations because of their tendency to lag environmental variation. Therefore, in spite of our exclusion of post-Chernobyl pulse data, we expect to see some evidence of disequilibration, and we expect to see this more pronounced in piscivores than in planktivores or benthivores.

The assimilation efficiency of animals for ^{137}Cs is known to be high except when food is rich in clay minerals to which ^{137}Cs strongly absorbs (Kolehmainen 1972; Eyman and Kitchings 1975). Its clearance rate in animal tissues also decreases with increasing animal size. Thus, we would expect that steady-state tissue concentrations will generally exceed concentrations found in food except when assimilation efficiency is abnormally low, or growth rate is high enough to bring about significant growth dilution. High concentrations of suspended clay minerals in water would be expected to reduce bioaccumulation factors for planktivores and benthivores by reducing the assimilation efficiency for ^{137}Cs through direct competition between the ingested clay and the gut membrane. These hypotheses will be tested by multiple linear regression on the global data set that we have compiled from a wide range of freshwater and marine sources.

Methods

Data on Cs in fish (either muscle or whole body) and Cs in water (dissolved or total) were obtained from primary literature as well as government monitoring reports, together with our own data for the Ottawa River. Concentrations of Cs in whole fish should be slightly lower than concentrations in muscle (hard tissues tend to be lower in Cs but comprise a small proportion of body mass), but these differences should not have a significant effect on the analysis because variability among systems spans orders of magnitude. For systems with relatively low concentrations of suspended sediment, there will be little difference between dissolved and total concentrations of Cs in water (e.g., in Lake Erie, a fairly turbid system, about 90% of the ^{137}Cs is dissolved). However, for most of the turbid systems (e.g., western basin of Great Slave Lake and White Oak Lake), dissolved concentrations were reported. Most data were for ^{137}Cs measured by γ-spectrometry using NaI or Ge crystals; however, some data for stable ^{133}Cs were also included. These were measured by γ-spectrometry following neutron activation. The isotope of Cs measured is coded in Table 1. For sites with data spanning several years, we averaged both water and fish Cs values over the same time span. For freshwater sites cation chemistry was obtained from the literature (usually determined by atomic absorption spectrometry) and for most marine sites cation chemistry was estimated by multiplying salinity measurements by the mean composition of seawater given in Broecker and Peng (1982). Concentrations of suspended inorganic sediments were obtained from the literature when available, but generally were calculated using the allochthonous sediment mass-balance approach outlined by Rowan et al. (1992). Fish yields and net primary production were obtained from the literature sources identified in Table 2, and represent averages from time intervals spanning from several years to decades. A detailed discussion on the statistical aspects of the ratio of piscivore yield to primary production was given by Rowan and Rasmussen (1992). Fish were placed in trophic (piscivore and nonpiscivore) and thermal habitat (epilimnetic vs. hypolimnetic) categories using Scott and Crossman (1973) for North American freshwater fish; Phillips and Rix (1985) and Wheeler (1969) for European freshwater fish; and Leim and Scott (1966), Carcasson (1977), Burgess and Axelrod (1973), and Smith and Heemstra (1986) for marine fishes. When lengths and/or weights were not included in the data sources, they were obtained from Bykov (1984) or the preceding sources. Mean annual temperature was obtained from climatic atlases as outlined in Rasmussen and Kalff (1987).

Data were analyzed by linear regression (SYSTAT, MGLH; Wilkinson 1989) using $\log_{10}$-transformed variables. To test for the effectiveness of the log transformations in removing heteroscedasticities and nonlinearities, the residuals from our models were examined to ensure that they were normally distributed about the predicted values, and that residuals were uncorrelated with the predicted Y values. No problems of this sort were found. The regressions were examined for serious collinearity effects using the condition index and the variance decomposition (Belsley et al. 1980, in Wilkinson 1989), and for significant leverage effects using the Cook statistic as outlined in SYSTAT (Wilkinson 1989). Thus, the models obtained fit the underlying assumptions of linear regression analysis.

Results and Discussion

Statistical Analyses

Because most of the data used in this analysis have not been published previously in readily accessible journals, we have included them in summary form (Tables 1–3).

The global data set (Table 1) was analyzed by log–linear regressions relating the concentration of ^{137}Cs in fish ($mBq \cdot kg^{-1}$) to concentrations of ^{137}Cs ($mBq \cdot l^{-1}$) and K ($\mu M \cdot L^{-1}$) in water for each trophic category (piscivore = 1, nonpiscivore = 0). Concentrations of ^{137}Cs in fish increased linearly with concentrations of ^{137}Cs in water, and the BAF values decreased significantly with the K concentration of the water. The BAF was significantly higher for piscivores than nonpiscivores, and the slope of the concentration of ^{137}Cs in fish relative to water was greater for nonpiscivores than for piscivores. The models obtained were

$$\begin{aligned}(1)\quad \log[^{137}Cs]_{fish} &= 3.956(0.053) \\ &+ [0.915(0.027) \\ &- 0.083(0.038)(\text{trophic level})]\log[^{137}Cs]_{water} \\ &- 0.541(0.016)\log[K]_{water} \\ &+ 0.382(0.054)(\text{trophic level}) \\ R^2 = 0.876,\ SE_{est} &= 0.305,\ N = 362\end{aligned}$$

and

$$\begin{aligned}(2)\quad \log\ ^{137}Cs\ BAF &= \\ &3.863(0.045) - 0.164(0.028)(\text{trophic level})\log[^{137}Cs]_{water} \\ &- 0.549(0.016)\log[K]_{water} \\ &+ 0.488(0.043)(\text{trophic level}) \\ R^2 = 0.817,\ SE_{est} &= 0.309,\ N = 362.\end{aligned}$$

A more detailed analysis of the effects of trophic structure of the pelagic food web and other physicochemical factors was possible for a large portion of the global data set. Although Equations (1) and (2) clearly show the importance of the trophic position of fish, the lower levels of the food web that link forage fish to primary production differ greatly among systems. This aspect of trophic structure is difficult

TABLE 1. Sampling location, fish species, trophic level, ^{137}Cs concentration of fish, ^{137}Cs and K concentration of water, and data source. (For trophic level, piscivores = 1 and nonpiscivores = 0.) *[^{133}Cs] in fish ($\mu g \cdot kg^{-1}$) and water $ng \cdot L^{-1}$).

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
			Freshwater		
Cable Lake, Michigan, USA					
Micropterus salmoides	1	33.7	5.5	90	1
Clinch River, Tennessee, USA					
Aplodinotus grunniens	1	8.7*	25.0*	33	2
Ictalurus punctatus	1	4.1*	25.0*	33	2
Lepomis macrochirus	0	3.4*	25.0*	33	2
Morone chrysops	1	16.0*	25.0*	33	2
Pomoxis annularis	1	12.9*	25.0*	33	2
Pomoxis annularis	1	17.6	29.4	33	2
Dewey Lake, Michigan, USA					
Micropterus salmoides	1	26.3	1.9	64	1
East Twin Lake, Colorado USA					
Oncorhynchus mykiss	0	1988.2*	580.0*	46	3
Elbe River, Germany					
Abramis brama	0	2.4	8.2	512	4
Anguilla anguilla	1	4.7	8.2	512	4
Leuciscus idus	0	1.8	8.2	512	4
Leuciscus rutilus	0	2.6	8.2	512	4
Lake Erie, central basin, Canada–USA					
Micropterus dolomieui	1	2.2	0.6	33	5–8
Morone chrysops	1	2.1	0.6	33	5–8
Oncorhynchus kisutch	1	0.9	0.5	33	5–8
Stizostedion vitreum	1	1.0	0.6	33	5–8
Lake Erie, eastern basin, Canada–USA					
Oncorhynchus mykiss	1	1.4	0.3	33	5–8
Lake Erie, western basin, Canada–USA					
Oncorhynchus kisutch	1	1.3	0.9	31	5–8
Oncorhynchus mykiss	1	1.9	0.8	31	5–8
Osmerus mordax	0	0.5	1.3	31	8,9
Perca flavescens	1	1.1	1.3	31	8,9
Stizostedion vitreum	1	0.9	0.8	31	5–8
Fair Lake, Michigan, USA					
Micropterus salmoides	1	41.1	8.9	243	1
Fine Lake , Michigan, USA					
Micropterus salmoides	1	22.2	5.2	83	1
Georgian Bay, Ontario, Canada					
Salvelinus namaycush	1	10.2	1.8	18	5,10–13,60
Stizostedion vitreum	1	43.6	4.1	18	5,10–13,60
Gleaston Beck, UK					
Salmo trutta	0	2.0	7.4	102	14
Great Slave Lake, Christie Bay, Canada					
Catostomus catostomus	0	1.3	1.9	22	15–18
Coregonus artedii	0	3.1	1.9	22	15–18
Coregonus clupeaformis	0	1.8	1.9	22	15–18
Esox lucius	1	4.4	1.9	22	15–18
Lota lota	1	2.9	1.9	22	15–18
Prosopium cylindraceum	0	2.0	1.9	22	15–18
Salvelinus namaycush	1	5.7	1.9	22	15–18
Great Slave Lake, McLeod Bay, Canada					
Coregonus artedii	0	19.3	3.6	11	15–18
Esox lucius	1	22.9	3.6	11	15–18
Prosopium cylindraceum	0	6.7	3.6	11	15–18
Salvelinus namaycush	1	23.8	3.6	11	15–18

TABLE 1. (*Continued*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
Great Slave Lake, western basin, Canada					
Coregonus artedii	0	0.4	1.3	26	15,17,18
Coregonus clupeaformis	0	0.5	1.3	26	15,17,18
Esox lucius	1	1.8	1.3	26	15,17,18
Lota lota	1	1.1	1.3	26	15,17,18
Stenodus leucichthys	1	1.1	1.3	26	15,17,18
Lake Huron, northern basin, Canada–USA					
Alosa pseudoharengus	0	3.7	1.5	22	6,9–13,19
Lota lota	1	5.8	1.5	22	6,9–13,19,20
Osmerus mordax	0	5.9	1.5	22	6,9–13,19
Perca flavescens	1	9.2	1.5	22	6,9–13,19
Lake Huron, southern basin, Canada–USA					
Alosa pseudoharengus	0	3.7	1.8	22	6,9,10,11,19,21
Ambloplites rupestris	1	7.2	1.2	22	5,7,10,11,21–28
Catostomus commersoni	0	2.7	1.2	22	5–7,9–11,19,21,22,25,28–38
Coregonus clupeaformis	0	2.5	1.1	22	5,11,21,31,33
Coregonus hoyi	0	2.7	1.5	22	6,9,10,11,19,21
Cyprinus carpio	0	1.0	1.2	22	5,10,11,21,24,31
Esox lucius	1	4.6	1.3	22	5,7,10,11,21–23,30,32–34,37,39
Ictalurus nebulosus	1	6.0	1.3	22	5,7,10,11,21–27
Ictalurus punctatus	1	3.9	1.2	22	5,11,19,21,28,29,34,37,38
Lota lota	1	3.1	1.8	22	5,10,11,19,21
Micropterus dolomieui	1	5.4	1.1	22	5,7,10,11,19,21,23,24,26,29,31,32,34–38
Morone chrysops	1	3.5	1.1	22	5,11,21,38
Oncorhynchus kisutch	1	8.5	1.2	22	5,11,19,21
Oncorhynchus mykiss	1	5.2	1.8	22	10,11,21,39
Perca flavescens	1	8.0	1.1	22	5,7,10,11,21,23–26,28,30–33
Stizostedion vitreum	1	6.2	1.2	22	5,19,11,21,28–33,35–38
Inarinjarvi, Finland					
Coregonus clupeaformis	0	50.5	55.5	8	39–42
Esox lucius	1	139.6	55.5	8	39–42
Lota lota	1	155.8	55.5	8	40–42
Perca fluviatilus	1	106.2	55.5	8	39–42
Salmo trutta	1	145.8	55.5	8	39–42
Salvelinus alpinus	1	121.2	55.5	8	39–42
Salvelinus salvelinus	1	116.9	55.5	8	39–42
Thymallus vulgaris	0	55.8	55.5	8	39–42
Kytajarvi, Finland					
Abramis blicca	0	4.8	10.4	47	40–42
Abramis brama	0	9.2	10.4	47	40–42
Esox lucius	1	16.3	10.4	47	40–42
Leuciscus rutilus	0	12.4	10.4	47	40–42
Lota lota	1	14.1	10.4	47	40–42
Lucioperca lucioperca	1	28.9	10.4	47	40–42
Perca fluviatilus	1	11.0	10.4	47	40–42
Lupton Beck, UK					
Salmo trutta	0	3.7	4.0	49	14
Lower Three Runs Creek, South Carolina, USA					
Aphredoderus sayanus	0	213.1	296.0	36	43
Esox niger	1	268.8	296.0	36	43
Gambusia affinis	0	263.7	296.0	36	43
Lepomis auritus	0	394.9	296.0	36	43
Lepomis marginatus	0	204.5	296.0	36	43
Micropterus salmoides	1	829.7	296.0	36	43
Notropis petersoni	0	323.2	296.0	36	43

TABLE 1. (*Continued*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
Melkutin, Finland					
Coregonus clupeaformis	0	51.8	16.7	24	40–42
Esox lucius	1	253.1	16.7	24	40–42
Leuciscus rutilus	0	86.2	16.7	24	40–42
Perca fluviatilus	1	250.1	16.7	24	40–42
Lake Michigan, USA					
Alosa pseudoharengus	0	5.9	2.5	29	6,7,9,12,13,19, 44–50
Catostomus commersoni	0	8.7	3.4	29	12,13,44,46,48–50
Coregonus clupeaformis	0	8.9	2.2	29	12,13,45,47–50
Coregonus hoyi	0	8.9	2.5	29	6,7,9,12,13,19,44–50
Cottus cognatus	0	7.2	2.0	29	6,7,9,12,13,19,45,47–50
Cyprinus carpio	0	8.5	3.4	29	12,13,44,46,48–50
Micropterus dolomieui	1	13.7	3.4	29	12,13,44,46,48–50
Oncorhynchus kisutch	1	18.6	2.8	29	12,13,44–50
Oncorhynchus mykiss	0	9.3	3.4	29	12,13,44,46,48–50
Oncorhynchus mykiss	1	11.3	2.6	29	6,7,9,12,13,19,44,46,48–50,76
Oncorhynchus tshawytscha	1	16.0	2.6	29	6,7,9,12,13,19,44,46,48–50,76
Osmerus mordax	0	7.5	2.5	29	6,7,9,12,13,19,44–50
Perca flavescens	1	15.4	2.6	29	6,7,9,12,13,19,44–50
Salmo trutta	1	16.3	2.6	29	6,7,9,12,13,19,44,46,48–50,76
Salvelinus namaycush	1	12.9	2.5	29	6,7,9,12,13,19,44–50
Muggelsee, Germany					
Abramis brama	0	3.4	4.8	102	4
Anguilla anguilla	1	3.1	4.8	102	4
Lucioperca lucioperca	1	10.0	4.8	102	4
Perca fluviatilus	1	7.0	4.8	102	4
Niemenjarvi, Finland					
Abramis blicca	0	3.0	30.3	94	40–42
Abramis brama	0	3.7	30.3	94	40–42
Esox lucius	1	11.1	30.3	94	40–42
Leuciscus rutilus	0	5.4	30.3	94	40–42
Lota lota	1	14.1	30.3	94	40–42
Perca fluviatilus	1	8.3	30.3	94	40–42
North Channel, Ontario, Canada					
Acipenser fluvescens	0	3.7	2.1	16	5,11,19,60,61
Salvelinus namaycush	1	8.2	2.3	16	5,11,19,60,61
Stizostedion vitreum	1	9.8	2.1	16	5,11,19,60,61
Northburn Beck, UK					
Salmo trutta	0	2.3	2.5	96	14
Oder River, Germany					
Anguilla anguilla	1	8.7	10.5	179	4
Aspius rapax	1	10.4	10.5	179	4
Esox lucius	1	11.4	10.5	179	4
Leuciscus rutilus	0	5.2	10.5	179	4
Tinca vulgaris	0	6.7	10.5	179	4
Lake Ontario, Canada–USA					
Alosa pseudoharengus	0	1.8	1.3	43	6–9,12,19,29,51–53
Ambloplites rupestris	1	9.1	1.2	43	5–9,12,19,51–53,79
Anguilla americanus	1	5.3	1.2	43	5–9,12,19,51–53,79
Aplodinotus grunniens	1	5.4	1.3	43	8,12,51–53
Catostomus commersoni	0	1.0	0.8	43	5,8,12,19,27,29,30–38,53–57
Coregonus clupeaformis	0	0.7	0.8	43	5,8,12,19,29,30,33–38,53–57
Cottus cognatus	0	1.9	1.3	43	8,12,51–53
Cyprinus carpio	0	1.3	1.0	43	5,8,12,22,24,26,27,51–54
Dorosoma cepedianum	0	3.8	1.1	43	5,8,12,25,51–54
Esox lucius	1	2.6	1.2	43	5,8,12,51–54
Salvelinus fontinalis × *S. namycush*	1	2.1	0.8	43	5,8,12,19,29,53,54

TABLE 1. (*Continued*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
Ictalurus natalis	1	1.8	1.0	43	5–9,12,19,23–27,51–54,58,79
Ictalurus punctatus	1	4.7	0.9	43	5,8,12,25,53
Lepisosteus osseus	1	4.5	1.3	43	8,12,51–53
Maxostoma macrolepidotum	0	4.0	1.3	43	8,12,51–53
Micropterus dolomieui	1	2.4	0.8	43	5,7,8,12,23,26–32,36,38,53–57
Micropterus salmoides	1	7.8	1.3	43	8,12,51–53
Morone americana	1	2.1	0.6	43	5,8,12,24,26,37,38,53,54,56,57
Morone chrysops	1	3.8	1.0	43	5–9,12,19,22,24,25,51–54
Oncorhynchus kisutch	1	4.2	1.2	43	5–9,12,19,51–53,79
Oncorhynchus mykiss	1	2.0	0.9	43	5,7,8,12,23–25,27,29,30,53–55
Oncorhynchus tshawytscha	1	5.9	1.3	43	8,12,51–53
Osmerus mordax	0	2.4	1.2	43	8,12,27,51–54
Perca flavescens	1	4.3	1.0	43	5–9,12,19,23,25–34,51–58,79
Salmo trutta	1	1.7	0.9	43	5,8,12,19,29,30,33–38,53–57
Salvelinus namaycush	1	1.5	0.9	43	5,8,12,26,28–30,32–38,53–57
Stizostedion vitreum	1	2.4	0.6	43	5,8,12,27,37,38,53,54,56,57
Ottawa River, Canada					
Catostomus commersoni	0	11.7	3.5	17	26,28–34,57,59–62
Coregonus clupeaformis	0	5.6	2.0	17	57,59,63
Esox lucius	1	26.9	3.5	17	28,31–33,57,59,61–63
Ictalurus punctatus	1	27.0	3.4	17	28,30,31,57,59,61
Lota lota	1	29.4	3.9	17	26,27,30,57,59–61
Moxostoma anisurum	0	9.6	3.2	17	28,57,59,60,63
Micropterus dolomieu	1	21.1	2.9	17	28,31,57,59,61,63
Perca flavescens	1	21.4	3.0	17	29,33,57,59,60,62,63
Stizostedion canadense	1	41.3	3.6	17	30,57,59,61
Stizostedion vitreum	1	54.9	3.6	17	26–34,57,59–63
Par Pond, South Carolina, USA					
Ictalurus natalis	1	1406.0	1221.0	36	64,65
Lepomis macrochirus	0	999.0	1221.0	36	64,65
Micropterus salmoides	1	1295.0	1221.0	36	64,65
Po River, Italy					
Barbus barbus	0	14.3	112.0	66	66
Chondrostoma soetta	0	50.3	112.0	66	66
Chondrostoma toxostoma	0	43.8	112.0	66	66
Leuciscus caphalus	0	21.3	112.0	66	66
Pond B, South Carolina, USA					
Dorosoma cependianum	0	459.0	760.0	36	67
Gambusia affinis	0	1750.0	760.0	36	67
Ictalurus natalis	1	332.0	760.0	36	67
Labidesthes sicculus	0	45.0	760.0	36	67
Lepomis gulosus	0	149.0	760.0	36	67
Lepomis macrochirus	0	246.0	760.0	36	67
Micropterus salmoides	1	381.0	760.0	36	67
Pomoxis nigromaculatus	1	431.0	760.0	36	67
Red Lake, Minnesota, USA					
Aplodinodus grunniens	1	52.6	37.0	179	68
Catostomus commersoni	0	22.7	37.0	179	68
Coregonus clupeaformis	0	40.7	37.0	179	68
Esox lucius	1	133.9	37.0	179	68
Lota lota	1	44.2	37.0	179	68
Perca flavescens	1	27.8	37.0	179	68
Perca flavescens	0	15.1	37.0	179	68
River Gary, UK					
Salmo trutta	0	136.9	48.7	8	14
Schnable Lake, Michigan, USA					
Micropterus salmoides	1	3.7	3.0	90	1

TABLE 1. (*Continued*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
Stechlinsee, Germany					
Anguilla anguilla	1	132.5	74.0	51	4
Coregonus albula	0	118.4	74.0	51	4
Esox lucius	1	186.5	74.0	51	4
Leuciscus rutilus	0	76.5	74.0	51	4
Perca fluviatilus	1	228.3	74.0	51	4
St. Lawrence River, Quebec, Canada					
Catostomus commersoni	0	1.5	1.1	40	8,12,53,54,56,57,59,62,63,69
Cyprinus carpio	0	1.2	1.0	40	8,12,53,54,56,57,62,63,69
Esox lucius	1	2.3	1.2	40	8,12,53,54,56,57,62,63,69
Ictalurus punctatus	1	2.6	1.3	40	8,12,53,54,56,57,62,63,69
Micropterus dolomieui	1	2.9	1.2	40	8,12,53,54,56,57,62,63,69
Moxostoma anisurum	0	1.3	1.0	40	8,12,53,54,56,57,62,63,69
Perca flavescens	1	2.9	1.2	40	8,12,53,54,56,57,62,63,69
Stizostedion vitreum	1	2.6	1.2	40	8,12,53,54,56,57,62,63,69
Suolijarvi, Finland					
Coregonus albula	0	53.3	29.2	22	40–42
Esox lucius	1	143.2	29.2	22	40–42
Leuciscus rutilus	0	65.9	29.2	22	40–42
Lota lota	1	80.5	29.2	22	40–42
Perca fluviatilus	1	100.1	29.2	22	40–42
Lake Superior, Canada–USA					
Osmerus mordax	0	7.4	2.8	14	6,9–13,19
Salvelinus namaycush	1	12.7	2.4	14	5,10–13,70
Salvelinus siscowet	1	14.3	2.3	14	5,10–13,70
Sutton Bingham, UK					
Salmo trutta	0	0.5	1.3	103	14
Trawsfynydd, UK					
Perca fluviatilus	1	92.5	18.9	9	14
Perca fluviatilus	1	960.0	228.0	10	14,71–73
Salmo trutta	0	473.3	228.0	10	14,71–73
Salmo trutta	0	62.9	18.9	9	14
Ullswater, UK					
Salmo trutta	0	10.7	7.9	12	14
White Oak Lake, Tennesee, USA					
Carassius auratus	0	19.5*	28.4*	45	74
Carassius auratus	0	1277.6	2153.4	45	74
Dorosoma cepedianum	0	12.9*	28.2*	45	2,74
Dorosoma cepedianum	0	1740.1	2153.4	45	74
Ictalurus melas	1	7.6*	28.0*	45	2
Lepomis gulosus	0	12.1*	28.4*	45	74
Lepomis gulosus	0	1357.5	2153.4	45	74
Lepomis macrochirus	0	10.1*	28.2*	45	2,74
Lepomis macrochirus	0	1480.4	2153.4	45	74
Lepomis microlophus	0	9.0*	28.4*	45	74
Lepomis microlophus	0	993.5	2153.4	45	74
Micropterus salmoides	1	14.3*	28.2*	45	2,74
Micropterus salmoides	1	1951.8	2153.4	45	74
Notemigonus crysoleucas	0	14.5*	28.4*	45	74
Notemigonus crysoleucas	0	2316.6	2153.4	45	74
Lake Winnipeg, Manitoba, Canada					
Coregonus clupeaformis	0	0.9	1.2	57	15,16
Stizostedion canadense	1	2.9	1.2	57	15,16
Wintergreen Lake, Michigan, USA					
Amia calva	1	8.2	10.2	249	2,75
Amia calva	1	5.2*	23.0*	249	2,75
Erimyzon succeta	0	7.7	10.2	249	2,75
Erimyzon succeta	0	6.4*	23.0*	249	2,75

TABLE 1. (*Continued*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
hybrid sunfish	0	5.4*	23.0*	249	2,75
hybrid sunfish	0	4.9	10.2	249	2,75
Ictalurus natalis	1	9.1	10.2	249	2,75
Ictalurus natalis	1	5.3*	23.0*	249	2,75
Ictalurus nebulosus	1	4.7	10.2	249	2,75
Ictalurus nebulosus	1	6.7*	23.0*	249	2,75
Micropterus salmoides	1	12.0*	23.0*	249	2,75
Micropterus salmoides	1	16.2	10.1	249	2,75
Perca flavescens	1	11.4	10.2	249	2,75
Perca flavescens	1	33.8*	23.0*	249	2,75
			Marine		
Atlantic Ocean, Faroe Islands					
Gadus callarias	1	0.3	3.5	10030	77–85
Melanogrammus aeglefinus	0	0.2	3.5	10030	77–85
Atlantic Ocean, Greenland					
Anarrhichas lupus	1	0.5	5.8	8840	84
Gadus morhua	1	0.5	5.0	8840	82,84,86–88
Hippoglossus vulgaris	1	0.3	6.5	8840	85
Mallotus villosus	0	0.2	7.2	8840	84,86,88,89
Salmo salar	1	0.3	5.7	8840	82,84,86,87
Salmo trutta	1	0.8	6.2	8840	83
Atlantic Ocean, Iceland					
Gadus morhua	1	0.5	3.6	10002	71–73,90
Melanogrammus aeglefinus	0	0.2	3.5	10002	72,90
Pleuronectes platessa	0	0.2	3.8	10002	73,90
Atlantic Ocean, Norway					
Gadus morhua	1	2.2	45.0	9492	72,90
Melanogrammus aeglefinus	0	2.6	45.0	9492	72,90
Atlantic Ocean, Spain					
Micromesistus poutassou	0	0.3	3.9	9917	91
Trachurus trachurus	1	0.4	3.9	9917	91
Trisotropis luscus	1	0.3	3.9	9917	91
Baltic Sea, Belt Sea, Baresback, Sweden					
Anguilla anguilla	1	2.9	20.4	2774	92–98
Gadus morhua	1	5.0	20.4	2774	92–98
Limanda limanda	0	2.3	20.4	2774	92–98
Pleuronectes flesus	0	2.2	20.4	2774	92–98
Pleuronectes platessa	0	2.6	20.4	2774	92–98
Baltic Sea, Belt Sea, Ringhals, Sweden					
Anarrhichas lupus	1	4.4	40.2	5287	92–98
Anguilla anguilla	1	2.4	40.2	5287	92–98
Gadus morhua	1	4.0	40.2	5287	92–98
Limanda limanda	0	2.9	40.2	5287	92–98
Limanda sp.	0	2.4	40.2	5287	92–98
Myoxocephalus quadricorni	0	4.1	40.2	5287	92–98
Pleuronectes flesus	0	1.3	40.2	5287	92–98
Pleuronectes platessa	0	2.5	40.2	5287	92–98
Baltic Sea, Bothnian Bay, Finland					
Clupea harengus	0	3.0	12.1	878	99–102
Esox lucius	1	7.8	12.1	878	99–102
Baltic Sea, Gottland Basin, Okarshamn, Sweden					
Anguilla anguilla	1	2.5	17.0	1983	92,101
Esox lucius	1	2.1	17.0	1983	92,101
Baltic Sea, Greifswalder Bodden, Germany					
Anguilla anguilla	1	7.7	47.3	1790	4
Clupea harengus	0	2.4	47.3	1790	4

TABLE 1. (*Continued*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
Esox lucius	1	17.6	47.3	1790	4
Leuciscus rutilus	0	2.9	47.3	1790	4
Lucioperca lucioperca	1	12.3	47.3	1790	4
Perca fluviatilus	1	12.9	47.3	1790	4
Pleuronectes flesus	0	4.0	47.3	1790	4
Baltic Sea, Gulf of Bothnia, Forsmark, Sweden					
Anguilla anguilla	1	3.1	14.0	1558	92,101
Esox lucius	1	4.9	14.0	1558	92,101
Perca fluviatilus	1	3.9	14.0	1558	92,101
Baltic Sea, Gulf of Bothnia, Okiluoto, Finland					
Clupea harengus	0	1.5	10.8	1674	99–102
Esox lucius	1	4.1	12.7	1674	99–102
Perca fluviatilus	1	7.0	14.0	1674	99–102
Rutilus rutilus	0	1.6	14.0	1674	99–102
Baltic Sea, Gulf of Bothnia, Seili, Finland					
Clupea harengus	0	1.9	13.0	1898	99–102
Esox lucius	1	4.9	13.0	1898	99–102
Baltic Sea, Gulf of Bothnia, Vassa, Finland					
Clupea harengus	0	2.7	15.6	1643	99–102
Esox lucius	1	7.1	12.3	1643	99–102
Baltic Sea, Gulf of Finland, Lovissa, Finland					
Clupea harengus	0	1.7	8.6	1224	99–102
Esox lucius	1	3.3	8.6	1224	99–102
Leuciscus rutilus	0	1.5	12.0	1224	99–102
Perca fluviatilus	1	6.5	12.0	1224	99–102
Baltic Sea, Gulf of Finland, Tvarmine, Finland					
Clupea harengus	0	2.5	14.3	1757	99–102
Esox lucius	1	4.7	13.2	1757	99–102
Bering Sea, Alaska, USA					
Oncorhynchus keta	1	1.0	18.5	8783	106
Gulf of California, Mexico					
Anisotremus davidsoni	0	36.0*	320.0*	10200	103
Bairdiella icistius	0	54.0*	320.0*	10200	103
Cynoscion xanthulus	1	39.0*	320.0*	10200	103
Mugil cephalus	0	51.0*	320.0*	10200	103
Thunnus alalunga	1	40.5*	320.0*	9492	103
Irish Sea, Chapelcross, UK					
Pleuronectes flesus	0	263.0	3993.3	8783	71–73
Salmo trutta	1	96.0	1815.0	8783	73
Irish Sea, west, Ireland					
Clupea harengus	0	86.0	1000.0	9633	104,105
Gadus morhua	1	75.0	1000.0	9633	104,105
Merlangus merlangus	1	97.0	1000.0	9633	104,105
Pleuronectes platessa	0	35.0	1000.0	9633	104,105
Irish Sea, Wylfa, UK					
Pleuronectes platessa	0	22.0	854.0	9633	71
Pleuronectes flesus	0	38.0	611.0	9633	72
North Sea, middle, UK					
Clupea harengus	0	13.0	123.9	9803	71,72,90
Gadus morhua	1	9.7	100.9	9803	71–73,90
Melanogrammus aeglefinus	0	6.7	100.9	9803	71–73,90
Merlangus merlangus	1	17.2	100.9	9803	71–73,90
Pleuronectes platessa	0	4.7	100.9	9803	71–73,90
North Sea, north, UK					
Clupea harengus	0	3.9	59.9	9917	71,72,90
Gadus morhua	1	6.5	59.8	9917	71–73,90

TABLE 1. (*Concluded*)

Location and species	Trophic level	^{137}Cs fish ($Bq \cdot kg^{-1}$)	^{137}Cs water ($mBq \cdot L^{-1}$)	K ($\mu m \cdot L^{-1}$)	References[a]
Melanogrammus aeglefinus	0	4.6	59.8	9917	71–73,90
Pleuronectes platessa	0	4.0	59.8	9917	71–73,90
Pollachius virens	1	3.3	56.9	9917	72,73,90
Pout	0	1.2	54.2	9917	72,90
North Sea, southern, UK					
Gadus morhua	1	7.1	39.4	9633	71–73,90
Merlangus merlangus	1	4.4	39.4	9633	71–73,90
Pleuronectes platessa	0	2.7	39.4	9633	71–73,90
Pacific Ocean, California, USA					
Thunnus alalunga	1	3.3	24.0	9492	107
Pacific Ocean, Gulf of Alaska, USA					
Oncorhynchus keta	1	0.9	18.5	8925	106
Oncorhynchus kisutch	1	1.0	25.3	9492	106
Oncorhynchus kisutch	1	1.2	18.5	9067	106
Onforhynchus nerka	1	1.0	18.5	8925	106
Pacific Ocean, Hawaii, USA					
Thunnus alalunga	1	2.1	12.9	9917	107
Pacific Ocean, Japan					
Argyrosomus argantatus	1	0.3	12.2	9237	108
Beryx splendens	1	1.0	12.2	9237	108
Chrysophrys major	0	0.4	13.9	9237	109
Ditrema temmincki	1	1.1	17.8	9237	109
Engraulis sp.	0	0.2	12.2	9237	110
Hyperoglyphe japonica	0	0.4	12.2	9237	108
Katsuwonus pelamis	1	0.5	12.2	9237	108
Konosirus punctatus	0	0.5	12.5	9237	109
Lateolabrax japonicus	1	1.6	12.2	9237	108
Lotella maximowiczi	1	0.6	12.2	9237	108
Mylio macrocephalus	0	0.6	11.5	9237	109
Paracaesio caeruleus	1	0.5	12.2	9237	108
Paralichthys olivaceus	0	0.4	12.2	9237	108
Pleuronectes platessa	0	0.3	12.2	9237	110
Sardinops melanosticta	0	1.1	19.8	9237	109
Scombrops boops	1	1.2	12.2	9237	108
Sebastes matsubarai	0	0.4	12.2	9237	108
Sebastodes guntherii	0	0.7	20.4	9237	109
Seriola quinqueradiata	1	0.5	13.3	9237	109
Thunnus alalunga	1	2.7	14.8	9633	107
Pacific Ocean, Samoa					
Thunnus alalunga	1	0.5	3.1	10058	107
Sea of Japan, Japan					
Gadus macrocephalus	1	1.3	16.6	9237	109
Limanda irrdorum	0	0.5	13.6	9237	109
Mugil cephalus	0	0.9	15.5	9237	109
Scomber japonicus	0	0.6	24.6	9237	109
Sillago sihama	0	1.4	16.9	9237	109
Trachurus japonicus	0	0.7	14.9	9237	109

[a](1) Kevern and Spigarelli 1971; (2) Nelson 1969; (3) Hakonson and Whicker 1975; (4) Ettenhuber and Rohnsch 1975; (5) Joshi 1984; (6) Wahlgren and Nelson 1974; (7) Alberts and Wahlgren 1981; (8) Weiler and Chawla 1968; (9) Marshall et al. 1975; (10) Tracy and Prantl 1983; (11) Basch et al. 1980; (12) Kramer 1964; (13) Weiler and Chawla 1969; (14) Preston et al. 1967; (15) Elliot et al. 1981; (16) Armstrong and Schindler 1971; (17) Fee et al. 1985; (18) Rawson 1950; (19) Joshi 1991; (20) Armstrong and Lutz 1977a; (21) Smith et al. 1977; (22) Gorman and Walsh 1976; (23) Gorman and Walsh 1977; (24) Gorman and Walsh 1978; (25) Gorman and Walsh 1979; (26) Pilar and Walsh 1980; (27) Pilar 1981; (28) Neil 1984; (29) Neil 1982; (30) Neil 1983; (31) Neil 1985; (32) Neil 1986; (33) Neil 1987; (34) Neil 1988; (35) Neil 1989; (36) Neil 1990; (37) Neil 1991; (38) Christiani 1992; (39) Hasanen and Miettinen 1963; (40) Kolehmainen et al. 1966; (41) Kolehmainen et al. 1967; (42) Jaakkola et al. 1967; (43) Shure and Gottschalk 1976; (44) Nelson et al. 1972; (45) Waller et al. 1974; (46) Bowen 1972; (47) Yaguchi et al. 1974; (48) Torrey 1976; (49) Klein 1975; (50) Risley and Fuller 1965; (51) Bowen and Noshkin 1973; (52) Bowen 1974; (53) Kramer 1962; (54) Roy et al. 1990; (55) Baweja et al. 1987; (56) Neal 1991; (57) Atomic Energy of Canada, unpublished data; (58) Knight and Wong 1974; (59) Merritt 1975; (60) Lambert and Gibson 1983; (61) Nowell 1985; (62) Lim 1988; (63) Lim 1991; (64) Harvey 1964; (65) Newman and Brisbin 1990; (66) Smedile and Queirazza 1976; (67) Whicker et al. 1989; (68) Gustafson 1967; (69) Hydro Quebec; (70) Armstrong

to quantify and model, but has important implications for contaminant biomagnification. Rowan and Rasmussen (1992) characterized these differences using a trophic efficiency measure, the ratio of the sustained commercial yield of piscivorous fish (i.e., the top of the food chain) to the net primary production of the phytoplankton (base of the food chain) (PY/PP), and showed that among-lake variation in the bioaccumulation of persistent organochlorines in Great Lakes fish was largely due to variation in the length of pelagic food webs. Thus we hypothesized that the bioaccumulation of ^{137}Cs by fish will increase with increasing food-chain length (decreasing PY/PP). For many of the systems in our data set we were able to obtain data on the mean annual commercial yield of piscivorous fish ($g\ C \cdot m^{-2} \cdot yr^{-1}$) as well as mean annual primary production ($g\ C \cdot m^{-2} \cdot yr^{-1}$) (Table 2). We were also able to characterize fish according to their thermal zone (i.e., epilimnetic = 1 vs. hypolimnetic = 0), and mean annual temperature (°C) of the site. We expected that the temperature regime might affect the bioaccumulation of ^{137}Cs because it has been shown to influence the clearance rate of Cs isotopes from body tissues, in addition to its overall effect on metabolism. Body size, another important determinant of ^{137}Cs clearance and metabolism was also included in this analysis.

In addition, for this data set we were able to calculate allochthonous sediment mass balances, and the suspended sediment concentrations that we estimated ranged widely, from 71 $mg \cdot L^{-1}$ in the highly turbid western basin of Great Slave Lake to as low as 0.2 $mg \cdot L^{-1}$ in basins from Canadian shield drainage, and as much as 20-fold lower in the open ocean (Table 2). This allowed us to test the hypothesis that we outlined above concerning the negative effect of suspended clay on the ^{137}Cs BAF.

The models obtained from the log–linear regressions were

$$\begin{aligned}(3)\quad \log[^{137}Cs]_{fish} = {} & 2.743(0.225) + [1.012(0.033) \\ & - 0.105(0.035)(\text{trophic level})]\log[^{137}Cs]_{water} \\ & - 0.546(0.040)\log[K]_{water} \\ & + 0.362(0.041)(\text{trophic level}) \\ & - 0.249(0.035)(\log PY/PP) \\ & + 0.016(0.003)(\text{mean annual temperature}) \\ & + 0.103(0.040)(\text{thermal zone}) \\ & - 0.133(0.030)(\log[\text{suspended sediment}]) \\ & R^2 = 0.897,\ SE_{est} = 0.192,\ N = 209\end{aligned}$$

$$\begin{aligned}(4)\quad \log\ ^{137}Cs\ BAF = {} & \\ & - [0.099(0.031)(\text{trophic level})]\ \log[^{137}Cs]_{water} \\ & - 0.541(0.037)\log[K]_{water} \\ & + 0.356(0.037)(\text{trophic level}) \\ & - 0.251(0.034)(\log PY/PP) \\ & + 0.016(0.003)(\text{mean annual temperature}) \\ & + 0.104(0.040)(\text{thermal zone}) \\ & - 0.135(0.030)(\log[\text{suspended sediment}]) \\ & R^2 = 0.946,\ SE_{est} = 0.191,\ N = 209.\end{aligned}$$

Body sizes (length or weight or their logarithms) were not significant in any of the regressions that we tested (Equations (1)–(4)).

For this data set, we were able to obtain data on other major ions, and on specific conductivity. Although we hypothesized on the basis of the chemical similarity of the hydrated ions of Cs and K, that K should be a more effective isotropic carrier than other ions, the strong correlations that exist among ions make it possible that effective predictive models could be established using a wide variety of chemical parameters. We first used stepwise elimination (SYSTAT backward elimination; critical $t = 1.5$ for variable entry and leaving) with all chemical parameters (Table 2) tested. This analysis showed that K was in fact the best chemical parameter selected, and that no significant improvement in predictive power could be obtained from the inclusion of more chemical constituents. However, owing to the strong correlation among different chemical constituents, strong predictive models could be developed using any of the parameters.

Comparison of ^{137}Cs at Reactor Sites to Some Remote Sites in Canada

While our analyses show that environmental concentrations of ^{137}Cs are an important determinant of equilibrium levels in fish, the data indicate that ^{137}Cs levels in fish at reactor sites need not be higher than in fish from remote sites influenced solely by long-range atmospheric deposition. For example, the mass-balance calculations of Joshi (1991) suggest that about 50% of the ^{137}Cs in the waters of Lakes Ontario and Huron is of reactor origin, yet these waters have among the lowest ^{137}Cs concentrations in Canada (Table 3). This suggests that among-system variability in ^{137}Cs concentrations of water and fish resulting from catchment and lake processes is much greater than the reactor-derived increment. (Table 3).

Systems with catchments on the Canadian Shield have strikingly higher ^{137}Cs concentrations in their water than systems with catchments on sedimentary rock. This can be seen by comparing the Ottawa River, MacLeod Bay, and Lake Superior (shield catchments) to Lake Ontario, Lake Winnipeg, and the west basin of Great Slave Lake (mainly sedimentary catchments). Within Great Slave Lake, a lake far removed from reactor inputs, the on-shield (MacLeod Bay) to off-shield (west basin) gradient is most striking, with Christie Bay, a mixed drainage, having intermediate concentrations of ^{137}Cs in its water (Table 3). While catchment retention of radiocesium is always very high, it would appear that shield catchments retain a lower fraction of the ^{137}Cs fallout than do sedimentary catchments.

The Ottawa River, with a very large contribution from shield drainage, contains the highest concentrations of ^{137}Cs in both water and fish of all of the Canadian sites. These levels are high throughout the river, and the values obtained

and Lutz 1977b; (71) Hunt 1982; (72) Hunt 1984; (73) Hunt 1986; (74) Kolehmainen 1972; (75) Eyman and Kevern 1975; (76) Spigarelli and Edwards 1975; (77) Aakrog et al. 1979a; (89) Aarkrog et al. 1981b; (79) Walsh and Wong 1975; (80) Aarkrog et al. 1982b; (81) Aarkrog et al. 1983b; (82) Aarkrog et al. 1985a; (83) Aarkrog et al. 1985c; (84) Aarkrog et al. 1987b; (85) Aarkrog et al. 1992; (86) Aarkrog et al. 1981c; (87) Aarkrog et al. 1982c; (88) Aarkrog et al. 1983c; (89) Aarkrog et al. 1979b; (90) Camplin and Aarkrog 1989; (91) Mitchell et al. 1988; (92) Notter 1986; (93) Aarkrog et al. 1982a; (94) Aarkrog et al. 1984; (95) Aarkrog et al. 1987a; (96) Aarkeog et al. 1981a; (97) Aarkrog et al. 1985b; (98) Aarkrog et al. 1983a; (99) Institute of Radiation Protection 1979; (100) Institute of Radiation Protection 1980; (101) Institute of Radiation Protection 1984; (102) Finnish Centre for Radiation and Nuclear Safety 1987; (103) Young and Folsom 1979; (104) McAulay and Doyle 1985; (105) Jefferies and Steele 1989; (106) Jenkins 1969; (109) Young et al. 1975; (108) Nakahara et al. 1980; (109) Suzuki et al. 1973; (110) Kurabayashi et al. 1980.

TABLE 2. Production, suspended sediment concentration, and ion chemistry.

Site	Primary production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Piscivore fish yield ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Total fish yield ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Piscivore fish yield/ primary production ($\times 10^3$)	Total fish yield/ primary production ($\times 10^3$)	Suspended sediment ($mg \cdot L^{-1}$)	Salinity (‰)	Ca ($\mu M \cdot L^{-1}$)	K ($\mu M \cdot L^{-1}$)	Mg ($\mu M \cdot L^{-1}$)	Na ($\mu M \cdot L^{-1}$)	References[a]
					Freshwater							
Lake Erie												
Central Basin	224	0.040 50	0.078 25	0.180 80	0.349 33	23.56		953	33	326	472	1–4
Eastern Basin	176	0.015 40	0.019 72	0.087 50	0.112 05	14.98		988	33	349	497	1–4
Western Basin	340	0.102 10	0.174 43	0.300 29	0.513 03	11.12		858	31	281	332	1–4
Georgian Bay	80	0.000 47	0.002 69	0.005 88	0.033 63	0.21		578	18	279	141	1,3,5–7
Great Slave Lake												
Christie Bay	112	0.003 54	0.004 40	0.031 59	0.039 25	1.87		547	23	207	262	8–11
McLeod Bay	59	0.001 14	0.001 29	0.019 41	0.021 85	0.23		74	11	42	44	8–11
Western Basin	136	0.004 46	0.012 44	0.032 82	0.091 46	70.70		610	26	225	287	8–11
Lake Huron												
Northern Basin	90	0.000 20	0.002 74	0.002 22	0.030 44	2.70		636	22	310	145	1,3,5–7
Southern Basin	90	0.003 59	0.007 23	0.039 89	0.080 33	4.12		717	22	325	195	1,3,5,12
Lake Michigan	144	0.001 00	0.019 98	0.006 94	0.138 75	1.40		847	29	446	185	1,3,6,7,13–15
North Channel	72	0.000 89	0.004 51	0.012 36	0.062 64	1.03		549	16	263	139	1,5
Lake Ontario	180	0.004 19	0.006 60	0.023 28	0.036 67	7.92		988	43	336	483	1,6,7
Lake Superior	50	0.000 27	0.005 03	0.005 40	0.100 60	1.39		332	14	118	52	1,3,5–7
Lake Winnipeg	169	0.016 72	0.023 39	0.098 96	0.138 41	4.91		499	57	354	261	11,16–19
					Marine							
Atlantic Ocean												
Faroe Islands	200	0.240 00	0.500 00	1.200 00	2.500 00	0.04	35.4	10 133	10 030	52 110	462 158	20–29
Spain	125	0.142 00	0.469 00	1.136 00	3.752 00	0.07	35.0	10 019	9 917	51 521	456 936	20,21
Iceland	250	0.407 00	1.230 00	1.628 00	4.920 00	0.05	35.3	10 105	10 002	51 963	460 853	20,21
Greenland	125	0.386 00	0.560 00	3.088 00	4.480 00	0.28	31.2	8 931	8 840	45 927	407 326	20,21,26–33
Norway	150	0.093 00	0.273 00	0.620 00	1.820 00	0.15	33.5	9 589	9 492	49 313	437 353	20,21
Baltic Sea												
Belt Sea, Baresback	158	0. 218 00	0.410 00	1.379 75	2.594 94	1.11	9.8	2 802	2 774	14 411	127 812	21,34–42
Belt Sea, Ringhals	158	0.218 00	0.410 00	1.379 75	2.594 94	1.11	18.7	5 341	5 287	27 468	243 612	21,34–42
Bothnian Bay	71	0.008 57	0.040 00	0.120 70	0.563 38	0.42	3.1	887	878	4 563	40 471	21,34,35,43–46
Gottland Basin, Okarshamn	101	0.016 33	0.170 00	0.161 68	1.683 17	0.26	7.0	2 004	1.983	10 304	91 387	21,35,36,45
Gulf of Bothnia, Forsmark	81	0.008 57	0.040 00	0.105 80	0.493 83	0.34	5.5	1 574	1 558	8 096	71 804	21,35,36,45
Gulf of Bothnia, Okiluoto	81	0.008 57	0.040 00	0.105 80	0.493 83	0.34	5.9	1 692	1 674	8 700	77 157	21,34,35,43–46
Gulf of Bothnia, Seili	81	0.008 57	0.040 00	0.105 80	0.493 83	0.34	6.7	1 918	1 898	9 863	87 471	21,34,35,43–46
Gulf of Bothnia, Vassa	81	0.008 57	0.040 00	0.105 80	0.493 83	0.34	5.8	1 660	1 643	8 538	75 721	21,34,35,43–46
Gulf of Finland, Lovissa	71	0.026 66	0.310 00	0.375 49	4.336 20	0.33	4.3	1 237	1 224	6 359	56 399	21,34,35,43–46
Gulf of Finland, Tvarmine	71	0.026 66	0.310 00	0.375 49	4.366 20	0.33	6.2	1 775	1 757	9 127	80 943	21,34,35,43–46

TABLE 2. (*Concluded*)

Site	Primary production ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Piscivore fish yield ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Total fish yield ($g\ C \cdot m^{-2} \cdot yr^{-1}$)	Piscivore fish yield/ primary production ($\times 10^3$)	Total fish yield/ primary production ($\times 10^3$)	Suspended sediment ($mg \cdot L^{-1}$)	Salinity (‰)	Ca ($\mu M \cdot L^{-1}$)	K ($\mu M \cdot L^{-1}$)	Mg ($\mu M \cdot L^{-1}$)	Na ($\mu M \cdot L^{-1}$)	References[a]
Bering Sea	200	0.111 00	0.339 00	0.555 00	1.695 00	0.29	31.0	8 874	8 783	45 633	404 715	20,21
Gulf of California	100	0.211 00	0.889 00	2.110 00	8.890 00	0.01	36.0	10 305	10 200	52 993	469 992	20,21
Irish Sea												
Chaple cross	200	0.113 00	0.260 00	0.565 00	1.300 00	0.29	34.0	8 874	8 783	45 633	404 715	20,21
Western-Wylfa	200	0.113 00	0.260 00	0.565 00	1.300 00	0.12	31.0	9 732	9 633	50 049	443 881	20,21
North Sea												
Middle	150	0.168 00	0.521 00	1.120 00	3.473 33	0.09	34.6	9 904	9 803	50 932	451 714	20,21
Northern	150	0.168 00	0.521 00	1.120 00	3.473 33	0.07	35.0	10 019	9 917	51 521	456 936	20,21
Southern	150	0.168 00	0.521 00	1.120 00	3.473 33	0.12	34.0	9 732	9 633	50 049	443 881	20,21
Pacific Ocean												
California	100	0.211 00	0.889 00	2.110 00	8 890 00	0.15	33.5	9 589	9 492	49 313	437 353	20,21
Gulf of Alaska	200	0.090 00	0.584 00	0.450 00	2.740 00	0.26	31.5	9 017	8 925	46 369	411 243	20,21
Hawaii	75	0.052 00	0.261 00	0.693 33	3.480 00	0.07	35.0	10 019	9 917	51 521	456 936	20,21
Japan	114	0.750 00	1.878 00	6.578 95	16.473 68	0.20	32.6	9.332	9 237	47 988	425 603	20,21
Samoa	75	0.052 10	0.261 00	0.694 67	3.480 00	0.04	35.5	10 162	10 058	52 257	463 464	20,21
Sea of Japan	106	0.514 00	0.753 00	4.849 06	7.103 77	0.20	32.6	9 332	9 237	47 988	425 603	20,21

[a](1) Rowan and Rasmussen 1992; (2) Kramer 1961; (3) Schelske and Roth 1973; (4) Weiler and Chawla 1968; (5) Basch et al. 1980; (6) Kramer 1964; (7) Weiler and Chawla 1969; (8) Fee et al. 1985; (9) Keleher 1972; (10) Rawson 1950; (11) Armstron and Schindler 1971; (12) Smith et al. 1977; (13) Klein 1975; (14) Risley and Fuller 1965; (15) Torrey 1976; (16) Brunskill et al. 1979; (17) Brunskill and Graham 1979; (18) Brunskill et al. 1980; (19) Manitoba Department of Natural Resources, unpublished data; (20) Gulland 1971; (21) Broecker and Peng 1982; (22) Aarkrog et al. 1979a; (23) Aarkrog et al. 1981a; (24) Aarkrog et al. 1982a; (25) Aarkrog et al. 1983a; (26) Aarkrog et al. 1985a; (27) Aarkrog et al. 1985b; (28) Aarkrog et al. 1987a; (29) Aarkrog et al. 1992; (30) Aarkrog et al. 1979b; (31) Aarkrog et al. 1981b; (32) Aarkrog et al. 1982b; (33) Aarkrog et al. 1983b; (34) Thurow 1978; (35) Zenkevitch 1963; (36) Notter 1986; (37) Aarkrog et al. 1981c; (38) Aarkrog et al. 1982c; (39) Aarkrog et al. 1983c; (40) Aarkrog et al. 1984; (41) Aarkrog et al. 1985c; (42) Aarkrog et al. 1987b; (43) Institute of Radiation Protection 1979; (44) Institute of Radiation Protection 1980; (45) Institute of Radiation Protection 1984; (46) Finnish Centre for Radiation and Nuclear Safety 1987.

TABLE 3. Levels of ^{137}Cs in water ($mBq \cdot L^{-1}$) and fish ($Bq \cdot kg^{-1}$) from several Canadian sites with (*) and without nuclear facilities (1978–80). See Table 1 for references.

	Lake Ontario*	Lake Huron*	Lake Superior	Ottawa River below NDP*	Above NDP*	Lake Winnipeg*	Great Slave Lake		
							Christie Bay	MacLeod Bay	Western Basin
Water	0.7	1.1	1.7	4.4	4.1ns	1.2	1.9	3.6	1.3
Planktivores									
Alosa pseudoharengus	1.1	2.4							
Coregonus artedii							3.1	19.3	0.4
Coregonus hoyi		2.0							
Osmerus mordax	1.5	4.3	4.5						
Average	1.3	2.9	4.5				3.1	19.3	0.4
Average BAF	1857	2636	2647				1632	5361	308
Benthivores									
Catostomus catostomus							1.3		
Catostomus commersoni	0.9	2.4		15.0	13.7ns				
Coregonus clupeaformis	0.6	2.4		12.3		0.9	1.8		0.5
Cottus cognatus	1.0								
Cyprinus carpio	1.0	1.0							
Maxostoma anisurum	2.2			13.3					
Prosopium cylindraceum							2.0	6.7	
Average	1.1	1.9		13.5	13.7	0.9	1.7	6.7	0.5
Average BAF	1629	1758		3076	3341	750	895	1861	385
Piscivores									
Ambloplites rupestris	5.3	6.5							
Anguilla americanus	3.3								
Aplodinotus grunniens	2.9								
Esox lucius	1.6	4.1		34.9	30.5ns		4.4	22.9	1.8
Hybrid Salvelinus	2.0								
Ictalurus natalis	5.0								
Ictalurus nebulosus		1.3							
Ictalurus punctatus	3.9	3.7							
Lota lota		4.2		42.7	28.5ns		2.9		1.1
Micropterus dolomieui	2.1	5.2		28.9	32.7ns				
Micropterus salmoides	4.3								
Morone americana	2.7								
Morone chrysops	2.8	3.4							
Oncorhynchus kisutch	2.6	7.7							
Oncorhynchus mykiss	1.6	3.2							
Oncorhynchus tshawytscha	3.2								
Perca flavescens	3.1	7.7		30.1	33.9ns				
Salmo trutta	1.4								
Salvelinus namaycush	1.3		9.9				5.7	23.8	
Salvelinus siscowet			12.5						
Stenodus leucichthys									1.1
Stizostedion canadense						2.9			
Stizostedion vitreum	3.0	5.9		74.1	56.0ns				
Average	2.9	4.8	11.2	42.1	36.3ns	2.9	4.3	23.4	1.3
Average BAF	4135	4372	6588	9577	8859	2417	2281	6491	1026

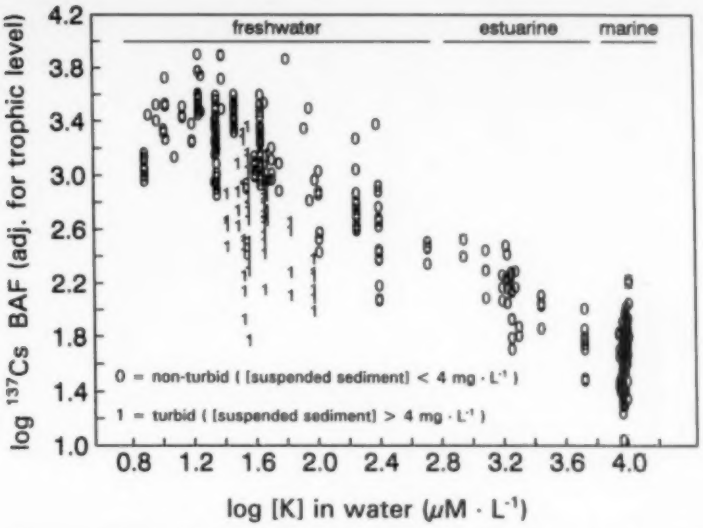

FIG. 1. Bioaccumulation of ^{137}Cs by fish in relation to concentrations of potassium and suspended sediment. BAF values are adjusted to nonpiscivore levels by subtracting 0.3 from piscivore estimates (see Equation (5)).

for fish in Holden Reservoir (upstream of the Rolphton reactor) are not significantly different from those below the dam near the reactor (Table 3). The Rolphton reactor was a small demonstration reactor operated by Ontario Hydro from 1965–83, and monitoring throughout this time showed no upstream–downstream differences. The dam at Rolphton clearly separates upstream from downstream fish populations, showing that high levels in upstream fish are not the result of upstream movements from reactor-influenced sites.

While piscivores in general bioaccumulate ^{137}Cs two- to three-fold relative to levels in forage species, the BAFs vary considerably from system to system. The soft waters of Lake Superior, Ottawa River, and MacLeod Bay have higher BAFs in all trophic categories than do Lake Ontario, Lake Huron, Christie Bay, and western Great Slave Lake (Table 3). This largely reflects the combined importance of the K and suspended sediment concentrations of the water, which were important predictors in Equation (4). BAFs for planktivores and benthivores are the lowest in the western basin of Great Slave Lake where the influence of suspended clay sediment is most pronounced.

Vulnerability of Softwater Systems to Radiocesium Contamination: Biogeochemical Factors

This analysis of global radiocesium data obtained from monitoring programs spanning the last 30 yr strongly supports the hypothesized effects of ions (especially K^+) as isotopic carriers by demonstrating that radiocesium bioaccumulation by fish, which occurs mainly through food, is sharply reduced by environmental K concentrations (Fig. 1). In fresh water, [K] ranges from <10 μM to around 0.5 mM, nearly three orders of magnitude, and in marine habitats ranges from <1 mM in estuaries to over 10 mM in the open ocean, about one order of magnitude. For each 10-fold difference in [K], bioaccumulation increases by around 3.5-fold (antilog of the regression coefficient for [K] in Equation (4)), and variability in [K] accounts for almost 10-fold variability in ^{137}Cs BAFs in freshwater systems. Therefore, fish from the softwater drainages found over large portions of northern Europe and Canada are much more sensitive to radiocesium fallout than those from hardwater, sedimentary drainages which in turn are more sensitive than marine systems.

However, the K-carrier mechanism is not the only factor contributing to high ^{137}Cs levels in fish from soft-water drainages. The low suspended sediment loads in soft waters (as low as 0.1 mg·L^{-1} compared with 10–100 mg·L^{-1} in sedimentary drainages) also contributes to about two-fold higher bioaccumulation (Equation 4). Finally, softwater lakes concentrate ^{137}Cs from atmospheric fallout more than lakes with sedimentary watersheds (Table 3). We hypothesize that this is a result of lower watershed retention of radiocesium owing to lower clay content in soils and surficial materials. Thus our analysis points to three important biogeochemical factors that make fish from soft waters much more vulnerable to radiocesium fallout than fish from hardwater sedimentary drainages and marine systems.

Vulnerability of Softwater Systems to Radiocesium Contamination: Trophic Factors

The generality of the biomagnification effect in food chains is further supported by the negative regression coefficient obtained in Equations (3) and (4) for PY/PP. This indicated that the BAF for fish from lakes with short food chains (high piscivore yields relative to primary production), have lower radiocesium BAFs than those from longer food chains (Fig. 2). Piscivore yields range from almost 1% of net primary production to less than 0.001% (Fig. 2; Table 2). Marine systems range from around 1 to 0.01% and thus appear to have, in general, shorter more direct food chains than freshwater systems wherein piscivore yields range from 0.03% (western Lake Erie) to <0.001% in the oligotrophic Laurentian Great Lakes.

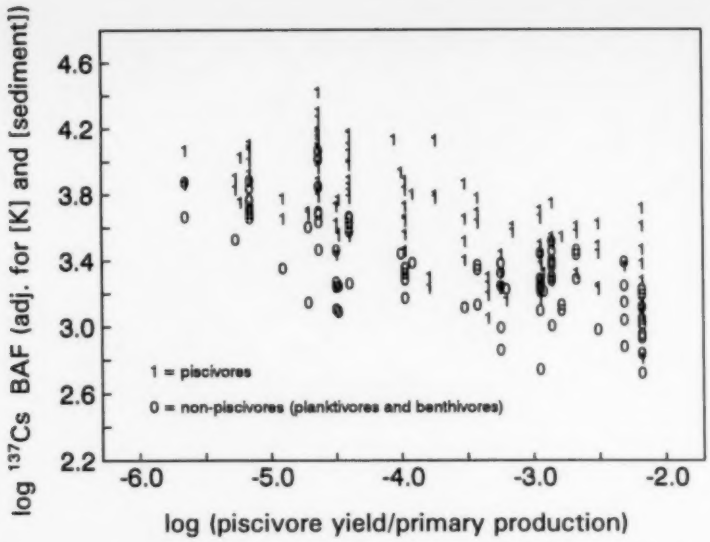

FIG. 2. Bioaccumulation of ^{137}Cs by fish in relation to trophic structure; piscivore yield/net primary production (PY/PP) characterizes the aquatic community in terms of the efficiency with which primary production is converted to fish, a function of food chain length. BAF estimates are adjusted for the effects of the two major physicochemical factors, [K], and [suspended sediment] using the coefficients in Equation (4); estimates were adjusted to 10 $\mu M \cdot L^{-1}$ K, and 1 $mg \cdot L^{-1}$ suspended sediment.

Variability in PY/PP probably reflects variable size structure of phytoplankton and its consequences for the size structure of zooplankton. Picoplankton are frequently processed by a web of microconsumers (the microbial loop), whereas large phytoplankton, such as diatoms, usually support large herbivorous zooplankton, such as *Diaptomus* or *Calanus* (Parsons et al. 1984). Plankton communities also vary considerably in the number of trophic levels in the zooplankton, including variation in the importance of macrozooplankton such as euphausiids, chaeotognaths, fish and invertebrate larvae, *Chaoborus*, or mysids (Rasmussen et al. 1990). Thus, the efficiency with which phytoplankton is converted to fish food can vary by orders of magnitude, with major consequences for fish productivity (Ryther 1969; Gulland 1970, 1971).

The almost 3000-fold range in PY/PP accounted for about seven-fold variability in the BAF of ^{137}Cs. Such an effect is consistent with the observation that piscivores generally have higher BAFs than forage fish, but in addition, shows that there is great variability in the trophic structure at the base of food webs that link forage fish to primary production, and that this variability has important consequences for radiocesium bioaccumulation. We found a very similar effect on the BAFs for PCBs and DDT in Great Lakes fishes (Rowan and Rasmussen 1992). While PY/PP seems to be a food web descriptor that explains among-system variation, its utility for prediction will be limited to situations where data on the yields from sustained commercial fisheries are available. For most inland waters such data are not available. We, therefore, present a model predicting ^{137}Cs BAFs with no PY/PP term below (Equation (5).

Softwater lakes tend to have the lowest PY/PP (e.g., Lake Superior, northern Lake Huron, and Georgian Bay; Table 2), and thus long food chains appear to be an additional contributing factor to high BAFs in fish from soft waters. In the sea, where PY/PP is highest, the shorter more direct food chains, combined with K concentrations of about 10 mM lead to the lowest BAFs recorded. Planktivores from the Japanese coast, the California coast, Greenland, and Iceland have BAFs less than 50, compared with upper Great Lakes values over 2000. Thus, high [K], short food chains, and the much greater volume and mixing potential make marine fish much less vulnerable to releases of ^{137}Cs.

In spite of the resilience of marine systems to radiocesium pollution, some marine sites such as those impacted by the fuel reprocessing plant at Sellafield, UK (e.g., Irish Sea and the adjacent North Sea) receive such high loadings of ^{137}Cs that ^{137}Cs concentrations in water exceed 1 $Bq \cdot L^{-1}$, and their fish exhibit levels of contamination on the same level as those from the Ottawa River and Georgian Bay where water concentrations are only a few millibecquerels per litre.

Effect of Clay on the Assimilation of Radiocesium from Food

Although many published studies on the distribution of radiocesium in aquatic communities have failed to demonstrate increases in tissue concentrations at higher trophic levels (Nelson 1969; Reichle et al. 1970; Thomann 1981), and indeed some studies even show lower radiocesium concentrations in fish tissues than in food (even for quasi-steady-state levels of radiocesium pollution) (Kolehmanien 1972; Mailhot et al. 1988), our analysis indicates that piscivores usually have about double the radiocesium concentrations seen in planktivores and benthivores. Although this appears to be true in general, there are a few examples within the data set that do not exhibit this pattern (Table 1). Kolehmanien (1972) presents an example where high clay content in White Oak Lake leads to this type of anomaly. He showed that

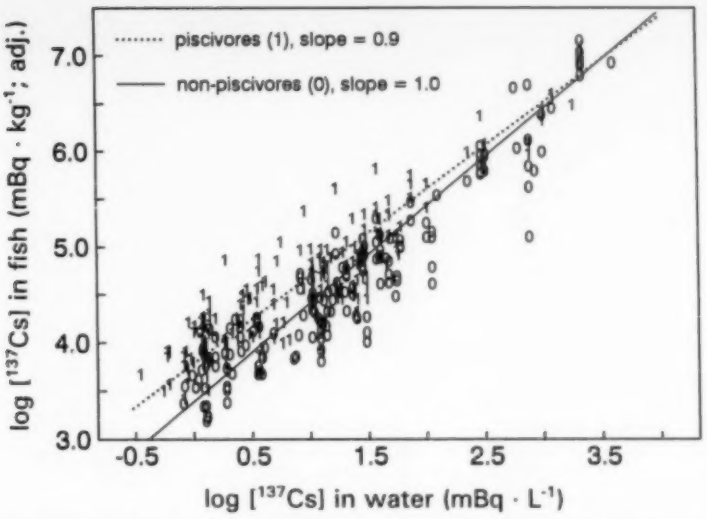

FIG. 3. Relationships between [^{137}Cs] in fish and water. Log–linear slope of 1 for nonpiscivores indicates that concentrations in fish at lower trophic levels track water concentrations closely; for piscivores slope <1 ($p < 0.01$) suggests that cesium levels in higher trophic level fish lag temporal variations in water concentrations slightly. [^{137}Cs] in fish were adjusted for the effects of the two major physicochemical factors, [K], and [suspended sediment] using the coefficients in Equation (4); estimates were adjusted to 10 $\mu M \cdot L^{-1}$ K, and 1 $mg \cdot L^{-1}$ suspended sediment.

bluegills (*Lepomis macrochirus*) have very low (<10%) assimilation efficiency for food items rich in clay (e.g., chironomid larvae and detritus) whereas food lacking clay had their radiocesium assimilated by the fish with around 60–70% efficiency. Our analysis of sites where we were able to estimate concentrations of suspended inorganic sediment by mass balance (Equation (3) and (4)), indicated that radiocesium bioaccumulation was much lower in lakes with high suspended sediment concentrations (Fig. 1). This effect was most clearly manifested in the comparison of the sediment-laden western basin of Great Slave Lake to the clearer, but chemically similar, Christie Bay waters of the same lake (Tables 2 and 3).

An alternative explanation for the effect of clay in our regressions is that some of the radiocesium concentrations in water were measured on unfiltered samples, with varying proportions of the radiocesium bound to particulates and unavailable. However, if this was the main factor then the slope of the water concentration term in Equation (1) should be significantly lower than one, and it is not. In addition, most of the water from turbid sites, where this effect would have greater significance, was filtered before analysis for radiocesium (e.g., Kolehmanien 1972; Elliot et al. 1981).

Disequilibrium between Piscivores and Environmental Concentrations

While we have tried to exclude data from pulse releases in this study, because of the biasing effect that disequilibrium between water and biota would have on estimates of BAFs, we predicted that year-to-year variations in releases from nuclear facilities and atmospheric fallout would lead to slight disequilibration at the top of the food web (piscivores), but that planktivores and benthivores would tend to track environmental variations very closely. The log–linear regression coefficient relating ^{137}Cs concentrations in nonpiscivorous fish to those in water was not significantly different from 1 (Equation (3); Fig. 3), which shows that BAFs estimated for nonpiscivores at high water concentrations were not significantly different from those estimated under low water concentrations. As hypothesized, fish low in the food chain appear to track variations in environmental ^{137}Cs concentrations closely enough to be essentially in equilibrium. For piscivores (Fig. 3) we observed log–linear slopes slightly but significantly <1, which we interpret as evidence of slight disequilibrium between tissue and water concentrations, resulting from the time lag required for ^{137}Cs released into the environment to be transmitted through the food web.

Results from tracer experiments and post-Chernobyl Europe provide more dramatic demonstrations of the disequilibrium associated with pulse inputs to aquatic systems. The fate of ^{134}Cs added to Lake 224 in the Experimental Lakes Area in northwestern Ontario was followed in the water and sediment (Hesslein et al. 1980; Hesslein 1987) and in the fish (Harrison et al. 1990). BAFs for fish in this system (BAFs have little meaning in disequilibrated systems) ranged from 3170 for littoral planktivores and 797 for pelagic piscivores 63 d following the addition, to 7040 in the pelagic piscivores after 1 yr (Harrison et al. 1990). Lake 224 is very low in K (about 9.5 $\mu M \cdot L^{-1}$) and suspended sediment (<1 $mg \cdot L^{-1}$) (Hesslein 1987) and predictions for planktivores and piscivores from Equation (5) are 4266 and 8356, respectively. As expected, the planktivores approached equilibrium quickly, while there was a substantial lag for the piscivores to reach equilibrium. Similar trends were observed in Europe following Chernobyl, with rapid increases (and decreases) in planktivores and slower, more moderate increases in piscivores (Elliott et al. 1992; Sundblad et al. 1991).

A Model for Equilibrated Systems

For truly equilibrated situations (at present, most North American systems) BAFs calculated for all fish should be independent of [^{137}Cs] in water, and a BAF model calculated without the interaction term between trophic level and [^{137}Cs] in water should apply. A simple model calculated without the interaction term and PY/PP, and including only the most robust predictors is

$$\begin{aligned}(5)\quad \log {}^{137}\text{CS BAF} = {} & 4.332(0.062) - 0.718(0.022)\log[\text{K}]_{\text{water}} \\ & + 0.292(0.034)(\text{trophic level}) \\ & - 0.233(0.027)(\log[\text{suspended sediment}]) \\ & R^2 = 0.873,\ SE_{\text{est}} = 0.275,\ N = 266.\end{aligned}$$

Temperature Effects

The temperature regime under which a fish lives exerts profound effects on all metabolic processes. Clearance rates of radiocesium are known to increase with temperature (Ugedal et al. 1992), but it cannot necessarily be inferred that equilibrium tissue levels will decrease with increasing temperature, because increases in feeding rates and/or basal metabolism could easily counter the effects of enhanced clearance. Thus it would be extremely difficult to predict a priori whether the BAFs for radiocesium would decrease, increase, or be unaffected by temperature. Although detailed data on the temperature regime were unavailable for most sites, our estimates of the mean annual air temperature combined with basic habitat information characterizing the fish as epilimnetic or hypolimnetic provides a reasonable description of the thermal regime experienced by the fish in our data set. Of course, within a region, our estimates of the effects of temperature cannot distinguish between large lakes that have lower mean annual temperatures than small lakes (Fee and Hecky 1992). The regressions (Equation (3) and (4)) suggest that the overall effect is for equilibrium levels of ^{137}Cs to increase with temperature because significant positive regression coefficients were obtained for mean annual temperature, and for the categorical variable describing the thermal zone inhabited by the fish (epilimnetic = 1, hypolimnetic = 0). This then suggests that the tendency for feeding and metabolic rates to increase with temperature overrides the tendency for enhanced clearance. This hypothesis should be further tested in laboratory studies.

Residual Variation and its Relation to Fish Bioenergetics

There is about twofold uncertainty in the predictions of fish radiocesium bioaccumulation in our models, despite their high predictive power (SE_{est} for predicting log[^{137}Cs] in fish and log(BAF) are 0.19). This uncertainty is about equal to the within-system variation observed among fish of the same trophic level (see Tables 1 and 3), variation observed among age-classes of species (D.J. Rowan, unpublished data) and seasonal variation within an age-class (Kolehmanien 1974). The natural variability is also much greater than any bias that may exist in the data owing to the mixture of analyses of whole fish or fish muscle. To explain such residual variation and thereby further increase predictive power, a much more detailed knowledge of the diet and the bioenergetic profile would be required for each age-class of each species at each site. Dynamic models such as that of Thomann (1981) indicate that the equilibrium tissue concentration of radiocesium depends on the concentration in food, the assimilation efficiency of Cs from the food, the biomass assimilation efficiency, the clearance rate of Cs from the body, the specific rates of food consumption, metabolism, and growth, and less importantly on direct uptake from water. Of these, the metabolic parameters are virtually never available for natural populations of fish, and reasonable variation in these parameters can easily lead to two-fold variation in the predictions made by such dynamic models. For this reason, such dynamic models are generally used for illustrative purposes or for simulation and sensitivity analyses, rather than prediction.

While it is virtually impossible to provide the site-specific ecological parameters necessary to make more accurate predictions of radiocesium bioaccumulation, it should be noted that there is considerable potential for using data on radiocesium levels in fish and their food organisms in combination with clearance models to estimate metabolic parameters, which are required for a wide range of ecological and management purposes. Site-specific estimates of such parameters made by traditional methods are very labor intensive and crude. Kevern (1966), Kolehmainen (1974), and, more recently, Forseth et al. (1992) have used this approach to estimate daily rations of fish. Furthermore, if growth rates can be supplied for the fish, which is usually possible, both daily rations and daily metabolic costs can be estimated. While this approach has only been employed in lakes with elevated radiocesium levels (Kevern (1966) and Kolehmainen (1974) studied carp (*Cyprinus carpis*) and bluegills at White Oak Lake near Oak Ridge, TN, and Forseth et al. (1991) studied salmonids in Norwegian lakes experiencing fallout from Chernobyl), modern γ counting technology can provide accurate and reasonably rapid estimates of radiocesium levels even in systems influenced only by long-range atmospheric fallout.

Linking Isotope Studies to Contaminant Bioaccumulation

Much of our resent research effort has been directed toward studying the factors that influence the BAFs for persistent contaminants (PCBs, DDT, methyl mercury, and, most recently, ^{137}Cs) with special emphasis on the effect of food-chain structure (Rasmussen et al. 1990; Rowan and Rasmussen 1992; Cabana et al. 1994). Because detailed characterization and quantitative descriptions of food chains are labour intensive and thus rarely carried out, one of our long-term goals is to use the BAFs for persistent substances as surrogate measures to quantify food-chain length. Radioisotopes such as ^{137}Cs seem to have potential for this type of purpose, when appropriate adjustments for K concentration, suspended sediment, and temperature are made. In addition to radioisotopes, we are also studying stable isotopes (^{15}N and ^{13}C) in the food webs of lakes including the Great Lakes, to investigate their possible use in quantitative description of trophic structure (Cabana and Rasmussen 1994).

We feel that there exists considerable unexplored potential for using steady-state radioisotope tracer approaches in ecological studies, and we are hoping that by analyzing basic patterns in the ecological behaviour of radioisotopes we can contribute both models useful in environmental management, and to broadening interest among ecologists and fisheries managers in radioisotopes as potential research tools.

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Fossil Pigment Records of Phytoplankton in Trout-stocked Alpine Lakes

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Paleolimnology, bioenergetics modelling, and mesocosm experiments were used to quantify changes in phytoplankton following introduction of trout into fishless alpine lakes in the Canadian Rocky Mountains. During the 1960s, Snowflake and Pipit lakes were stocked with brook (*Salvelinus fontinalis*), cutthroat (*Oncorhynchus clarkii*) and rainbow trout (*O. mykiss*) either singly or in combination. Stocked trout eliminated large invertebrates (*Daphnia* spp., *Hesperodiaptomus arcticus*, *Gammarus lacustris*), but the fish died within 15 yr. High performance liquid chromatographic analysis of carotenoids and chlorophylls in sediments inferred that algal abundance increased 4- to 10-fold shortly after fish stocking. In contrast, phytoplankton composition and biomass were constant in nearby, unstocked Harrison Lake, as inferred from fossils. Pigment analysis of mesocosms showed that phytoplankton were sensitive to moderate fertilization: 11 μg $P \cdot L^{-1}$ resulted in four- to six-fold increases in algal biomass. Bioenergetics modelling was used to estimate phosphorus (P) excretion from trout. The flux of excreted P was highly correlated ($r^2 = 0.76$, $p < 0.0001$, $N = 12$) to changes in algal biomass, as estimated from fossil pheophytin *b*. Consequently, we infer that nutrient recycling by stocked trout was one of several mechanisms that contributed to increased algal biomass.

La paléolimnologie, la modélisation bioénergétique et des expériences sur le mésocosme ont été employées pour quantifier les changements intervenus dans le phytoplancton à la suite de l'introduction de truites dans des lacs alpins dépourvus de poisson dans les montagnes Rocheuses canadiennes. Au cours des années 60, les lacs Snowflake et Pipit ont été ensemencés avec de l'omble de fontaine (*Salvelinus fontinalis*), de la truite fardée (*Oncorhynchus clarkii*) et de la truite arc-en-ciel (*O. mykiss*), individuellement ou en association. Les poissons ainsi introduits ont éliminé les invertébrés de grande taille (*Daphnia* spp., *Hesperodiaptomus arcticus*, *Gammarus lacustris*), mais les poissons sont morts au cours des 15 ans qui ont suivi. L'analyse par chromatographie liquide à haute performance des caroténoïdes et des chlorophylles des sédiments indique que l'abondance des algues a augmenté de 4 à 10 fois peu après l'ensemencement. Par contre, la composition du phytoplancton et la biomasse sont demeurées constantes dans un lac non ensemencé situé à proximité, le lac Harrison, comme l'indique l'analyse des éléments fossiles. L'analyse de pigments des mésocosmes a montré que le phytoplancton était sensible à la fertilisation modérée : 11 μg $P \cdot L^{-1}$ ont fait augmenter de quatre à six fois la biomasse des algues. La modélisation bioénergétique a été employée pour estimer l'excrétion du phosphore (P) par les truites. La quantité de phosphore excrétée était fortement liée ($r^2 = 0{,}76$, $p < 0.0001$, $N = 12$) aux changements de la biomasse des algues, comme le montre l'analyse de la phéophytine *b* fossile. Par conséquent, nous supposons que le recyclage des nutriments par les poissons introduits dans ces lacs a constitué l'un de plusieurs mécanismes qui ont contribué à l'augmentation de la biomasse des algues.

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Twenty percent of all lakes in Canada's Rocky Mountain National Parks have been stocked with exotic trout and related species (Donald 1987; Nelson and Paetz 1992). Many of these 305 lakes were naturally fishless before introduction of popular game fish such as rainbow trout (*Oncorhynchus mykiss*), cutthroat trout (*O. clarkii*), and brook trout (*Salvelinus fontinalis*). Size-selective predation by planktivorous trout often eliminated large-bodied invertebrate predators (*Hesperodiaptomus* spp.), herbivores (*Daphnia* spp.), and zoobenthos (*Gammarus lacustris*) from alpine food webs (Anderson 1972, 1974a, 1980; Donald et al. 1994). However, trout did not reproduce in headwater lakes that had small outflows and populations gradually declined

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(Donald 1987). In several lakes, *Hesperodiaptomus* have not recolonized even 15 yr after the fish disappeared (Paul and Schindler 1994). Despite intensive study of fish and invertebrates, little is known of the impact of trout introduction on phytoplankton biomass or composition.

Food-web theory predicts that stocked fish should increase algal production both by eliminating large, effective herbivores (Carpenter et al. 1985, 1987; Benndorf 1990) and by increasing nutrient supply through recycling (Lamarra 1975; Brabrand et al. 1990). McQueen et al. (1986) suggested that the effects of herbivory should be strongest in oligotrophic waters. Elser and Goldman (1991) refined this prediction when they found that algae in ultra-oligotrophic systems were extremely sensitive to changes in the abundance of large *Daphnia*, although grazing by *Diaptomus* was not important. Because large *Daphnia* spp. are usually eliminated by stocked trout in alpine lakes (Anderson and Donald 1978; Pechlaner 1984), fish stocking should increase the algal standing crop, particularly of small edible taxa. In addition, introduced trout may directly enhance nutrient supply and algal production, both by excreting nutrients and by decomposing after death (Carpenter et al. 1993).

We used paleoecological analyses of fossil pigments, mesocosm experiments, and bioenergetics modelling to reconstruct the historical changes in phytoplankton biomass before and after the introduction of trout to two alpine lakes in Banff National Park. Snowflake and Pipit lakes were naturally fishless, but were stocked with trout during the 1960s. Our unstocked reference basin, Harrison Lake, has naturally reproducing bull trout (*S. confluentus*) and was used to document natural lake variability. Concentrations of most fossil pigments are directly correlated to algal standing stock (Leavitt and Findlay 1994) and provide reliable historical reconstructions of phytoplankton populations during fish manipulations (Leavitt et al. 1989, 1993; Hurley et al. 1992).

Methods

Site Description and History

Snowflake, Pipit, and Harrison lakes are unproductive headwater ecosystems in the eastern Front ranges of the Canadian Rocky Mountains in Banff National Park, Alberta (51°36′N, 115°50′W). Current morphological and chemical conditions are summarized in Table 1 and by Anderson and Donald (1978). Waters are clear (Secchi depth 5–10 m), cold (T_{max} < 14°C; 9–10 mo ice cover) and poorly stratified. Algal abundance is limited by low nutrient concentrations (<6 μg total phosphorus (TP)·L^{-1}) and by low water residence time (Anderson and Donald 1978; D.W. Schindler, unpublished data).

All lakes lie at or above permanent tree line (ca 2130 m) in undisturbed, limestone basins (Anderson and Donald 1978; Table 1). Snowflake and Pipit lakes lie over 200 m above a fire road, 1.5 km distant, and have not been subject to local fires since the 1920s (Beder 1967). Harrison Lake is isolated from the road by 2.5 km and was probably last burned ca 1700 (Beder 1967).

Snowflake and Pipit lakes were originally fishless. The natural planktonic food webs included *Hesperodiaptomus arcticus* as the top predator, with either *Daphnia pulex* (Snowflake Lake) or *D. middendorffiana* (Pipit Lake) as the largest herbivore (Fig. 1a; Anderson 1972, 1975). *Gammarus lacustris* is an important benthic invertebrate in these lakes, feeding on both benthos and occasionally zooplankton (Anderson and Raasveldt 1974). In contrast, Harrison Lake contains naturally reproducing populations of bull trout. Although *Hesperodiaptomus* is absent from Harrison Lake, large herbivores (*D. pulex*), zoobenthos (*G. lacustris*), and cyclopoid copepods (*Diacyclops bicuspidatus thomasi*) are common (Fig. 1c).

Like other alpine lakes, Snowflake and Pipit lakes were stocked with trout during the 1960s to improve sport fishing (Mayhood 1992). Rainbow trout were stocked to Snowflake Lake (1960, 1963–65) and Pipit Lake (1964–66; Table 2). In addition, Snowflake Lake received eastern brook trout (1960, 1963–64) and cutthroat trout (1966) (Anderson 1975; Anderson and Donald 1978). Harrison Lake was never stocked according to Banff Park records (T. Hurd, Canadian Parks Service, Banff, AB, personal communication).

Invertebrate communities changed dramatically with the introduction of trout (Anderson 1972, 1975; Anderson and Donald 1978). *Hesperodiaptomus arcticus*, *Daphnia pulex*, and *Gammarus lacustris* were eliminated from Snowflake Lake by trout by 1968 (Fig. 1b). Elimination of the top invertebrate predator apparently allowed small herbivorous copepods (*Diaptomus tyrelli*), rotifers (*Kellicota longispina*, *Synchaeta oblongata*), and predacious cyclopoid copepods (*Acanthocyclops vernalis* and *Diacyclops bicuspidatus thomasi*) to flourish (Anderson 1972; Anderson and Donald 1978). In Pipit Lake, *H. arcticus* and *D. middendorffiana* gave way to *Acanthocyclops vernalis* by 1968. The quantitative response of *Gammarus* populations to trout introduction is unknown, although R.S. Anderson (New Serepta, AB, personal communication) reports that they were greatly reduced in abundance.

Trout did not reproduce in either Snowflake or Pipit Lake and populations were eliminated by 1984 or earlier (Anderson and Donald 1978). Periodic sampling during 1972–77 (Anderson and Donald 1978) and 1990–93 (Paul and Schindler 1994; D.W. Schindler, unpublished data) revealed that *Daphnia pulex* and *Gammarus* had recolonized Snowflake Lake by 1975, although *D. bicuspidatus thomasi* has remained the dominant copepod in place of *H. arcticus*. In Pipit Lake, *H. arcticus* and *Daphnia* were still absent by 1977, but both species were well established by 1990 (Paul and Schindler 1994). Currently, the invertebrate community of Pipit Lake is similar to the premanipulation composition, whereas Snowflake Lake still lacks *H. arcticus* and has 100- to 1000-fold higher rotifer biomass than Pipit Lake (Paul and Schindler 1994). *Gammarus* are currently present in the littoral zones of both lakes, but are much less common in Pipit Lake than in Snowflake Lake.

Sediment Samples

Sediments were sampled from the ice over the deepest portion of each lake in April 1991 using a freeze corer (Swain 1973). Frozen cores were prepared for fine-interval sectioning by removing the outermost 5 mm of sediment and freeze-drying the cleaned core for 24 h (Leavitt et al. 1989). Sections (5 mm thick) were isolated manually at −8°C within 3 h of freeze-drying sediments. Isolated samples were freeze-dried for a further 2 h and stored under a nitrogen atmosphere in the dark at −20°C for 24 h before further analysis (Leavitt et al. 1989).

Bulk sediment accumulation rates (mg dry weight·cm^{-2}·yr^{-1}) were estimated from ^{210}Pb activity profiles using

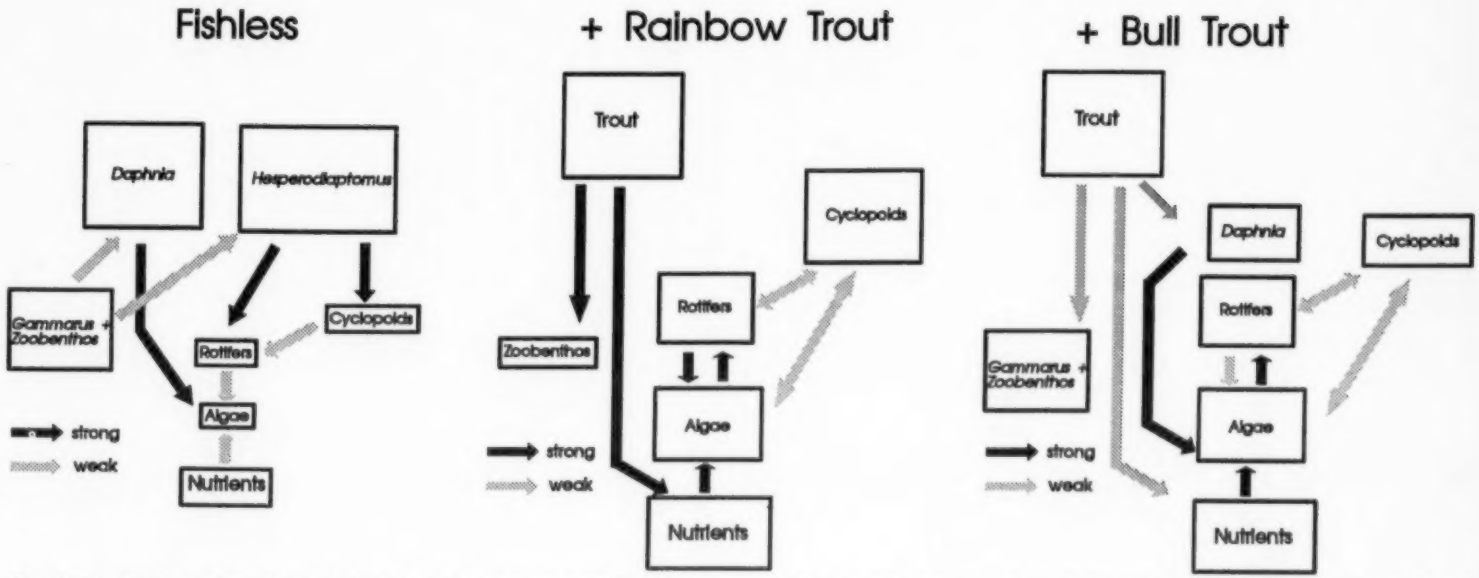

FIG. 1. Food-web configuration of alpine lakes before trout stocking (A), after stocking (B), and with natural populations of benthivorous bull trout (C). Solid arrows indicate strong effects and dashed arrows indicate weaker interactions.

TABLE 1. Mean time-weighted limnological conditions for the epilimnion of alpine lakes during the 1991 ice-free season.

Feature	Lake		
	Snowflake	Pipit	Harrison
Grid reference	11U/NH808167	11U/NH788188	11U/NH825119
Elevation (m)	2320	2217	2243
Surface area (ha)	7.1	10.6	8.4
Max. depth (m)	13.0	20.6	8.4
Mean depth (m)	6.1	12.6	5.4
Volume (m^3), $\times 10^4$	43.6	133.7	45.8
NO_3 ($\mu g \cdot L^{-1}$)	43	46	22
NH_4 ($\mu g \cdot L^{-1}$)	6	5	3
TDN ($\mu g \cdot L^{-1}$)	107	91	52
TP ($\mu g \cdot L^{-1}$)	4	5	6
TDP ($\mu g \cdot L^{-1}$)	3	3	5
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	0.63	0.83	0.82
Si ($mg \cdot L^{-1}$)	0.95	1.00	1.24
Cl ($mg \cdot L^{-1}$)	0.52	0.42	2.36
SO_4 ($mg \cdot L^{-1}$)	12.81	9.03	32.78
Na ($mg \cdot L^{-1}$)	1.97	1.55	0.64
K ($mg \cdot L^{-1}$)	0.33	0.29	0.24
Ca ($mg \cdot L^{-1}$)	24.75	25.58	34.78
Mg ($mg \cdot L^{-1}$)	10.11	9.37	10.83
Conductivity ($\mu S \cdot cm^{-2}$)	204	195	244
pH	8.07	8.11	8.09
Alkalinity ($mg \cdot L^{-1}$ as HCO_3^-)	201.7	204.7	198.0
Secchi depth (m)	5–8	4–10	4–8
Absorbance (@ 425nm)	0.052	0.022	0.028
Turbidity (NTU)	0.55	0.62	0.61

TABLE 2. Stocking history of Snowflake and Pipit lakes (modified from Anderson 1975; Anderson and Donald 1978).

Year	Species	Number stocked
	Snowflake Lake	
1960	*S. fontinalis*	1000
	O. mykiss	1000
1963	*S. fontinalis*	1000
	O. mykiss	500
1964	*S. fontinalis*	4000
	O. mykiss	1000
1965	*S. fontinalis*	5000
	O. mykiss	5000
	O. clarki	5000
1966	*S. fontinalis*	4000
	O. clarki	1000
	Pipit Lake	
1964	*O. mykiss*	4000
1965	*O. mykiss*	4000
1966	*O. mykiss*	4000

the distillation technique of Eakins and Morrison (1978) and the constant rate of supply model (Oldfield and Appleby 1984). Sediment age at each depth was estimated from sediment accumulation rates by integrating total sediment accumulation and calculating the length of time required for the observed mass accumulation. At each depth, sediment density was estimated by measuring sediment sample volume and dry mass (Leavitt and Findlay 1994). Standard errors (SE) of estimated age were generated using errors from slopes of unsupported (i.e., total - background) $\log_{10}$ ^{210}Pb activity versus mass accumulation plots. This procedure assumes collection of complete sediment profiles and underestimates sediment age if sediment–water interfaces are not collected.

In Snowflake Lake only, sediment age was also estimated by direct γ spectroscopic measurement of ^{137}Cs activity. This isotope is present in lake sediments after 1954 ± 2 yr, and results from open-air nuclear testing beginning in 1952 (Ritchie and McHenry 1990). Onset of activity (1954 ± 2 yr) and activity maxima in 1958 and 1963–64 are often used as stratigraphic markers. The ^{137}Cs activity in sediment samples from eight burial depths was measured by Dr. M. Stephenson and associates (AECL Research, Whiteshell Laboratory, Pinawa, MB) using a high-purity germanium intrinsic p-type well detector (Princeton Gamma-Tech) scanning the 662 keV photon peak. Because of insufficient aliquot size, sediments between 0 and 2.5 cm depth were not examined for ^{137}Cs activity. Sediment ages between 1954 and 1990 were estimated by assuming a constant rate of sediment accumulation in recent sediments.

Sedimentary pigments were extracted, filtered, and dried under nitrogen gas following the procedures of Leavitt et al. (1989). Carotenoid, chlorophyll, and derivative concentrations were quantified using a Waters high performance liquid chromatography (HPLC) system following the reversed-phase procedure of Mantoura and Llewellyn (1983), as modified by Leavitt et al. (1989). An internal reference standard (3.2 $mg \cdot L^{-1}$ of injection solvent) of Sudan II (Sigma Chemical Corp., St. Louis) was injected in each sample. This dye runs at a central, unique position on the chromatogram, has carotenoid-like absorption characteristics

TABLE 3. Main indicator pigments used in this study, their taxonomic specificity, and location of principal sources. P = pelagic or planktonic; L = littoral, benthic, or attached; T = terrestrial; S = sediments (modified from Leavitt 1993). Upper case letters indicates a quantitatively more important source than lower case.

Pigment	Source	Location
Alloxanthin	Cryptophytes	P
β-carotene	All plants, some bacteria	P L t
Echinenone	Cyanobacteria	P l
Fucoxanthin	Siliceous algae	P L
Lutein	Chlorophytes, euglenophytes, tracheophytes	P L t
Myxoxanthophyll	Colonial and filamentous cyanobacteria	P l
Zeaxanthin	Cyanobacteria	P l
Chlorophyll *a*	All plants	P l t
Chlorophyll *b*	Chlorophytes, euglenophytes, tracheophytes	P l t
Pheophorbide *a*	Chlorophyll *a* derivative (grazing)	P l s
Pheophytin *a*	Chlorophyll *a* derivative (general)	P L T s
Pheophytin *b*	Chlorophyll *b* derivative (general)	P L T s

(λ_{max} = 485, 442.5 nm in acetone), and was used to correct for dilution and injection errors (Leavitt and Findlay 1994).

Pigments isolated from sediments were compared with those from unialgal cultures. Spectral characteristics, chromatographic mobility, and functional group assays (Liaaen-Jensen 1971) were used to identify pigments from all sources (Leavitt et al. 1989). Acid derivatives of chlorophyllous pigments were created either by aqueous–alcohol extraction (chlorophyllides) or by acidification following the procedures of Leavitt et al. (1989). We restrict our analysis to carotenoids characteristic of cryptophytes (alloxanthin), diatoms (diatoxanthin), and chlorophytes + cyanobacteria (lutein–zeaxanthin), as well as the major *a* and *b*-phorbins (Table 3). Lutein from green algae and zeaxanthin from cyanobacteria could not be distinguished on our HPLC system. However, we infer that large cyanobacteria were rare because pigments specific to colonial cyanobacteria (e.g., myxoxanthophyll) were not recovered. Similarly, fucoxanthin from siliceous algae and one unknown carotenoid-like compound were not reliably separated by HPLC and diatoxanthin was used to estimate diatom biomass.

Not all fossil pigments were positively identified. The dominant compounds in all sediment cores were a series of unknown derivatives also seen in sediments from other unproductive montane (Quesnel Lake, British Columbia) and high Arctic ecosystems (ponds; P.R. Leavitt, unpublished data). These nonfluorescent compounds have sharply defined absorbance spectra with single, symmetrical peaks at either 380 or 440 nm, and may be stable carotenoid degradation products. Ongoing characterization of these compounds by mass spectroscopy will be presented elsewhere.

Organic content of sediment samples was estimated by weight loss on ignition at 500°C (Dean 1974). Pigment concentration was expressed as nmoles of pigment per gram organic matter. Recent changes in fossil pigment concentration were tested for significance using two-tailed *t*-tests, following correction for autocorrelation (Box et al. 1978). For each pigment, stratigraphies were divided into a pre-stocking and post-stocking era using fish stocking data (Table 2) and sediment dates estimated from either ^{137}Cs (Snowflake Lake) or ^{210}Pb analyses (all lakes). In unstocked Harrison Lake, 1960 was used to define eras equivalent to pre- and post-stocking. Autocorrelation coefficients were calculated for pre- and post-stocking data using the SYSTAT statistics system

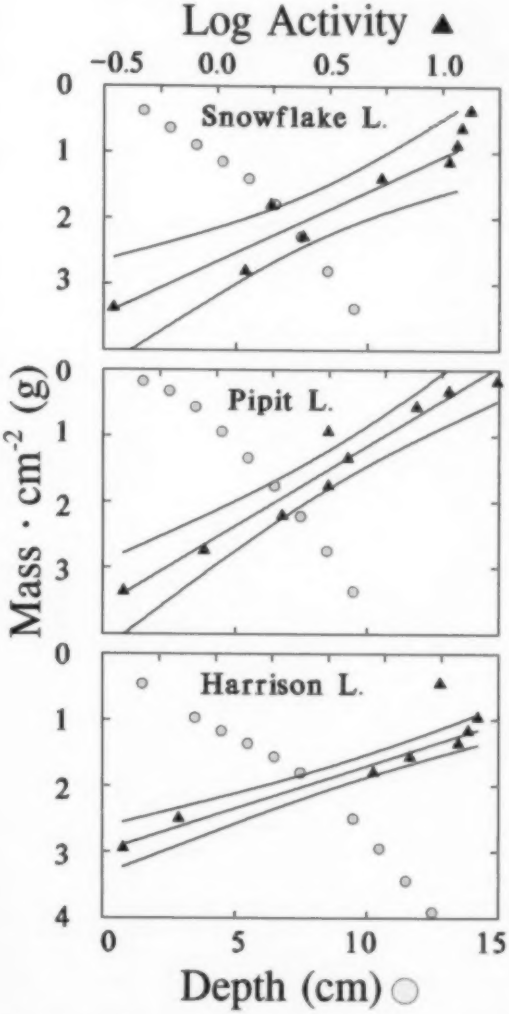

FIG. 2. Log_{10} activities of ^{210}Pb in sediments (dpm·(g dry wt)$^{-1}$; triangles) and sediment age (yr; circles) as a function of sediment accumulation (g·cm^{-2}) in Snowflake, Pipit, and Harrison lakes.

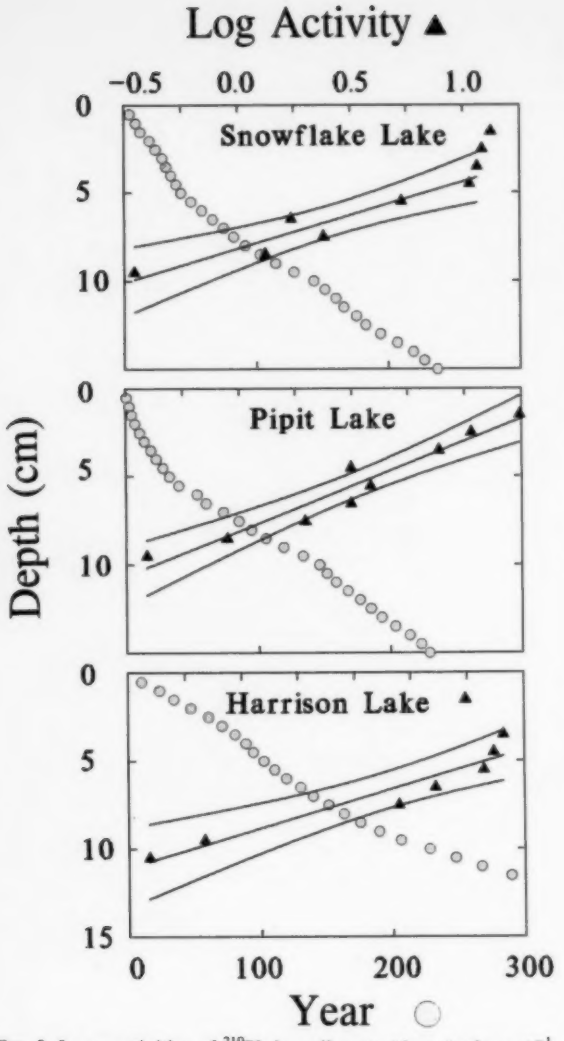

FIG. 3. Log_{10} activities of ^{210}Pb in sediments (dpm·(g dry wt)$^{-1}$; triangles) and sediment age (yr; circles) as a function of burial depth (cm) in Snowflake, Pipit, and Harrison lakes.

(Wilkinson 1989) and were used to correct *t*-statistics before the *t*-test (Box et al. 1978). In Harrison Lake, there were too few post-1960 samples to estimate autocorrelation coefficients, and *t*-tests were conducted with uncorrected *t*-statistics. Consequently, *t*-tests in Harrison Lake are regarded as lenient and may detect more significant differences than actually exist (Box et al. 1978).

Sediments were sampled for zooplankton remains using the procedure of Kitchell and Kitchell (1980). However, preliminary analyses indicated that zooplankton fossils were too sparse (<1 remain·(g dry wt.)$^{-1}$) to be accurately quantified while retaining high temporal resolution and analyses were discontinued.

Mesocosm Fertilization

To examine the effect that increased P concentrations would have on phytoplankton communities, six floating mesocosms of 2250 L were fertilized with 16 μg P·L^{-1} (as H_3PO_4) and 480 μg N·L^{-1} (as NH_4NO_3) every week and were compared with six unfertilized bags. Bags (1 m^2 surface area, closed at bottom) were filled with epilimnetic water and were suspended in Snowflake Lake from a floating PVC frame in July 1992 (Paul and Schindler 1994). Densities of both *Hesperodiaptomus* and *Daphnia* were usually below detection limits during the experiment.

Changes in algal abundance and community composition were estimated weekly using HPLC to quantify carotenoid and chlorophyll standing crops in open water and bags. Full analysis of algal community change is reported elsewhere (Paul and Schindler 1994; A.J. Paul, unpublished data). We report only the results of the initial sampling date, by which time the majority of algal biomass increase had occurred.

Fish Populations and P Excretion Estimates

To estimate the potential impact of nutrient recycling by fish, we reconstructed trout population size in Snowflake Lake from existing stock, growth, and diet records for rainbow and brook trout (Anderson 1975; Anderson and Donald 1978). We combined species and assumed that population mortality rates were 30% per year (Anderson and Donald 1978), that the maximum life-span was 15 years (Scott and Crossman 1973), and that no successful reproduction occurred (Anderson and Donald 1978). Annual growth rates of trout were calculated from von Bertalanffy growth-in-length curves (Prager et al. 1989) and length–mass regressions from fish caught from Snowflake Lake in 1973 and 1977 (Anderson and Donald 1978). Growth records were not available for Pipit Lake and we were not able to estimate trout population change for that lake.

Phosphorus excretion by fish in Snowflake Lake was estimated using an energy and mass balance model that accounts for changes in fish growth, respiration losses, and digestive losses of P in response to environmental temperature and body mass (Kraft 1992). We used water temperatures at 3 m depth (2–9°C annual range) to simulate the thermal histories of introduced trout. This method is an extension of a widely applied and corroborated fish growth model based on bioenergetic principles (Hewett and Johnson 1987).

The amount of urinary P excretion (U_p) was calculated as $U_p = C_p - G_p - F_p$ where C_p is the amount of P consumed, G_p is P assimilated into body tissue through growth, and F_p is P lost in fecal material.

The mass of prey consumed by stocked trout was calculated from growth curves using the bioenergetics model with physiological parameters for lake trout (*Salvelinus namaycush*) (Stewart et al. 1983). Consumption of P by fishes (C_p) was estimated by assuming that the invertebrate P content was equivalent to 0.18% of wet mass (Nakashima and Leggett 1980). Diets of brook trout were composed of about 95% invertebrates (Trichoptera, *Gammarus*, chironomids, terrestrial insects; Anderson and Donald 1978) which were assumed to have a caloric density of 800 cal·(g wet mass)$^{-1}$ (Cummins and Wuycheck 1971). The amount of P accrued in growth (Gp) was based on the assumption that P is 0.5% of fish wet mass (Davis and Boyd 1978). Phosphorus lost in fecal material (F_p) was calculated as 28% of C_p by assuming a P assimilation efficiency of 72% (Nakashima and Leggett 1980).

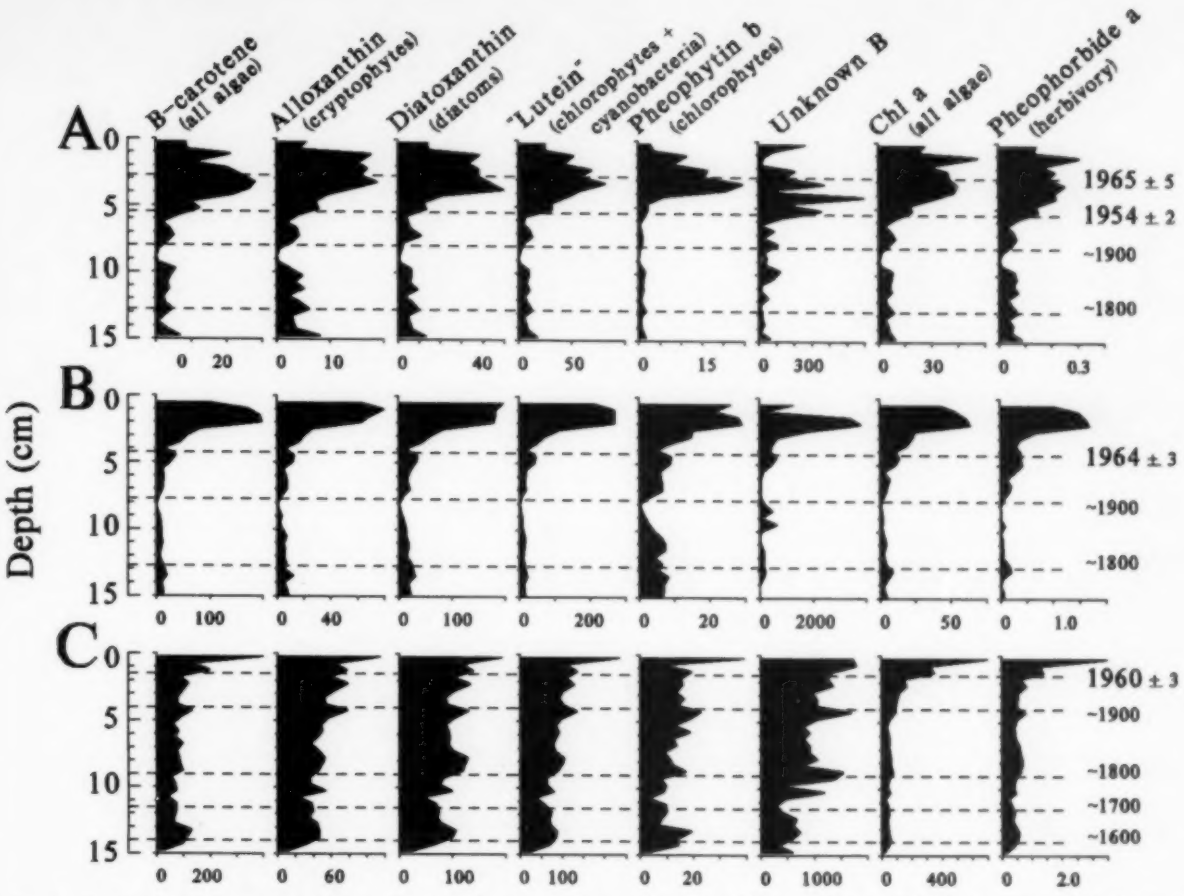

FIG. 4. Fossil pigment concentration profiles (nmol pigment·(g organic matter)$^{-1}$) for (A) Snowflake Lake, (B) Pipit Lake, and (C) Harrison Lake, 0–15 cm burial depth. All dashed lines indicate approximate sediment age based on ^{210}Pb analysis, except 1954 in Snowflake Lake, which is based on ^{137}Cs dating. Error estimates are standard errors of the mean.

Results

Sediment Description and Dating

Sediments of all three lakes were moderately organic (Pipit, 13.9 ± 1.7%; Snowflake, 28.4 ± 3.0%; Harrison, 12.4 ± 4.2%; mean ± SD), considering the low algal production (Anderson 1974a; Anderson and Donald 1978) and sparse terrestrial vegetation associated with these near-treeline sites. Occasional laminae were observed in the upper 40 cm of cores from all lakes. Snowflake Lake sediments were the least patterned with weak laminae only near 17 cm depth. In contrast, sediments from Pipit Lake showed distinctive light and dark couplets below 9 cm and occasional laminae between 2 and 7 cm. Harrison Lake sediments were intermediate. Live chironomids were collected from the surface sediments of Snowflake Lake, but not from Pipit or Harrison Lake.

Unsupported ^{210}Pb activities declined exponentially with accumulated mass (Fig. 2) and burial depth (Fig. 3) in Pipit Lake. Exponential decay was also noted in cores from Snowflake and Harrison lakes, but only in sediments deeper than 3–4 cm. Estimates of bulk sediment accumulation rate were similar in Snowflake Lake (23.9 ± 3.4 mg·cm^{-2}·yr^{-1}; mean ± SE) and Pipit Lake (29.0 ± 2.7 mg·cm^{-2}·yr^{-1}), but were higher than rates determined from duplicate cores in Harrison Lake (15.0 ± 0.9 mg·cm^{-2}·yr^{-1}; $N = 2$). Sediment depth–age relationships were similar in Snowflake and Pipit lakes, but not Harrison Lake (Fig. 3). In all three lakes, the relationship between estimated sediment age and burial depth was nonlinear in deeper sediments (Fig. 3). However, because of higher variability in accumulation rate estimates

TABLE 4. Depth distribution of ^{137}Cs activity in the sediments of Snowflake Lake.

Depth (cm)	Weight (g)	^{137}Cs Activity (Bq·(g dry wt)$^{-1}$)	2 SD (%)
2.5	0.6149	0.219	22
3.5	0.4746	0.130	48
4.5	0.4449	0.066	83
5.0	0.6875	0.051	73
5.5	0.9073	nd[a]	—
6.0	0.8255	nd	—
6.5	0.8451	nd	—
7.5	0.7546	nd	—

[a]Not detected.

TABLE 5. Mean fossil pigment concentrations before and after introduction of trout to Snowflake Lake (1960) and Pipit Lake (1964), and in reference Harrison Lake (no fish added). p = probability that post-stocking fossil concentrations are different from pre-stocking concentrations (Snowflake Lake, Pipit Lake), or that post-1961 concentrations are different from pre-1960 concentrations (Harrison Lake).

Pigment (group)		Snowflake pre-1960 (n = 19)	Snowflake post-1961 (n = 11)	Snowflake p	Pipit pre-1964 (n = 21)	Pipit post-1965 (n = 9)	Pipit p	Harrison pre-1960 (n = 26)	Harrison post-1961 (n = 4)	Harrison p[b]
β-carotene	mean	3.2	17.4	0.0001	11.1	105.4	0.034[a]	86.3	215.0	0.171
(all algae)	SD	1.9	7.6		6.0	74.9		26.7	143.6	
Alloxanthin	mean	3.4	12.1	0.0001	5.8	40.0	0.050[a]	46.4	78.9	0.076
(cryptophytes)	SD	2.0	5.3		2.9	29.0		14.5	24.9	
Diatoxanthin	mean	5.9	29.1	0.0001	18.5	113.9	0.044[a]	96.5	145.5	0.096
(diatoms)	SD	3.3	14.0		8.7	79.0		26.9	41.5	
Lutein–zeaxanthin	mean	8.2	48.1	0.0001	15.6	149.2	0.040[a]	83.7	147.4	0.120[a]
(chlorophytes, cyanobacteria)	SD	4.3	18.7		8.3	107.1		23.7	59.1	
Pheophytin *b*	mean	0.9	10.7	0.003	5.3	17.4	0.004[a]	13.5	22.5	0.285
(chlorophytes)	SD	0.5	8.2		2.4	9.0		5.2	13.8	
Unknown B	mean	48.4	203.0	0.019	148.0	1411.2	0.024	866.7	1527.7	0.009
(unknown origin)	SD	39.4	183.1		172.6	1358.4		371.3	279.8	
Chlorophyll *a*	mean	3.9	22.6	0.0001	8.1	70.1	0.002	63.4	388.6	0.064[a]
(all algae)	SD	1.8	8.1		4.8	42.0		33.0	234.4	
Pheophorbide	mean	17.5	64.4	0.001	49.6	472.4	0.030[a]	178.8	2333.6	0.132[a]
(grazing derivative)	SD	8.5	33.5		29.4	352.7		129.0	2134.0	

[a]Time series autocorrelated at a lag = 1. The t-statistic was calculated after correction of variance for autocorrelation (Box et al. 1978).

[b]Autocorrelation function not tested for post-1960 dates in Harrison Lake owing to insufficient data.

(Fig. 2), depth–age relationships were more variable in Snowflake Lake than in Harrison Lake or Pipit Lake.

In Snowflake Lake, significant ^{137}Cs activity was detected only in sediment samples above 5.5 cm depth (Table 4). Activities declined in an approximately logarithmic fashion between 2.5 and 5.0 cm, and did not show significant maxima corresponding to nuclear testing in 1958 or 1963–64. Consequently, only the onset of activity between 5.5 and 5.0 cm depth can be used as a chronological marker (1954 ± 2 yr).

Fossil Pigment Stratigraphies

Snowflake Lake

Premanipulation fossil concentrations were low, constant, and similar for all identified pigments (Fig. 4a). For all pigments, fossil concentration increased near 1954 ± 2 yr. Most concentration profiles showed a historical maximum near 1965 (±5 yr), as determined by ^{210}Pb and ^{137}Cs dating. In particular, concentrations of lutein–zeaxanthin and *b*-phorbins from chlorophytes increased between 8- and 23-fold near the time of trout stocking. In contrast, alloxanthin from cryptophytes and diatoxanthin from diatoms increased between four- and sixfold. Pheophorbide *a* was in extremely low concentration (<1 nmol·(g organic matter)$^{-1}$) when analyzed by standard spectrophotometric methods, although in-line HPLC fluorometry revealed that pheophorbide *a* also increased fourfold in the early 1960s. Unidentified carotenoid derivatives (e.g., unknown B) showed larger, but irregular increases. In all cases, mean fossil pigment concentrations above 5.5 cm (1955–90) were significantly greater (t-test; $p < 0.02$, df = 10; Table 5) than those in deeper sediments (ca 1750–1955).

Most fossil pigment concentrations declined to near-pre-manipulation levels in the most recent sediments of Snowflake Lake. In contrast, chlorophyll *a* and pheophorbide *a* remained abundant in surface sediments. Labile pigments such as these often show substantial degradation shortly after deposition and may be in unusually high abundance in the most recent sediments (Furlong and Carpenter 1988; Hurley and Armstrong 1990, 1991; Leavitt 1993).

Pipit Lake

Concentrations of all fossil pigments increased significantly (t-test, $p < 0.05$, df = 8) following introduction of rainbow trout to Pipit Lake in 1964–66 (Fig. 4b, Table 5). As in Snowflake Lake, premanipulation concentrations of all pigments were similar, constant and low before 5- to 25-fold increases in both carotenoids and chlorophylls. In Pipit Lake, the response of pheophytin *b* from chlorophytes was less than that of other pigments, and less than that observed for chlorophyte pigments in Snowflake Lake. Again, concentrations of most pigments peaked at intermediate depths and declined in the most recent sediments. However, the extent of the decline was less than in Snowflake Lake, with most pigments exhibiting surface sediment concentrations three-fold greater than in deep-core samples.

Harrison Lake

Fossil pigments in the Harrison Lake core showed little systematic change with time, except for a gradual decrease in concentration with burial depth (Fig. 4c). Concentrations of most pigments were highest in the uppermost 0.5 cm, usually 50–100% greater than in older samples. In particular, labile chlorophyll *a* and pheophorbide *a* were characterized by rapid losses between 0 and 1 cm depth, typical of post-depositional degradation (Hurley and Armstrong 1990, 1991). Unlike Snowflake and Pipit lakes, mean fossil pigment concentrations in recent sediments of Harrison Lake

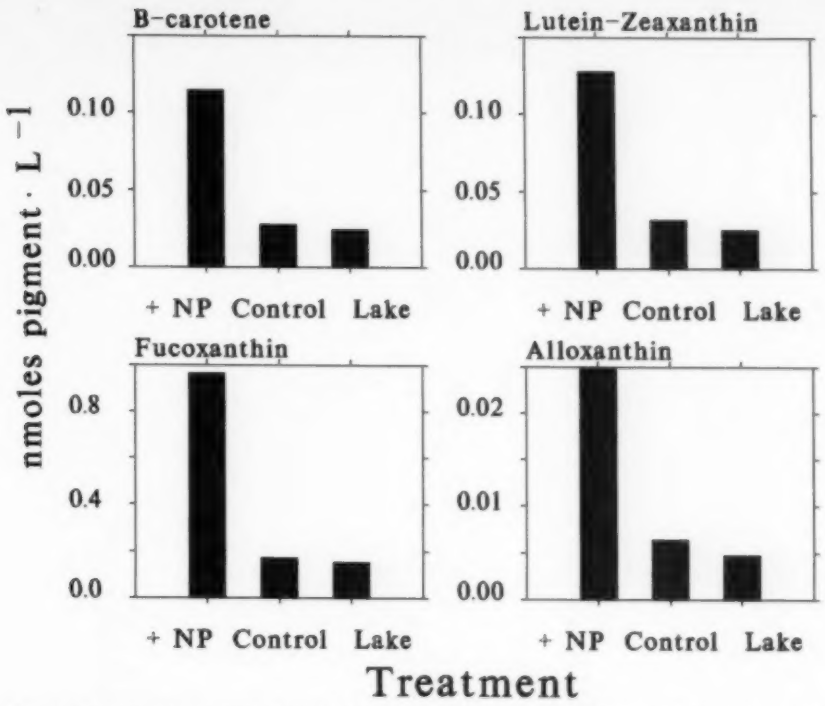

FIG. 5. Carotenoid concentrations in fertilized mesocosms (+NP), control mesocosms, and in Snowflake Lake after 7 d incubation.

(1960–90) were not significantly different (*t*-test, $p > 0.05$, df = 3) from those of older sediments (1600–1960; Table 5), except one unknown compound.

Mesocosm Experiments

Fertilization of mesocosms increased total P concentrations from 5.9 ± 0.5 to 17.0 ± 1.2 μg P·L^{-1} (mean ± SD) and resulted in four- to six-fold increases in concentrations of all major carotenoids within 7 d (Fig. 5). However, the relative composition of algal pigments did not change as a result of short-term fertilization. Fucoxanthin from diatoms and chrysophytes accounted for 75–80% of the total carotenoid abundance, while β-carotene (all algae; 10–13%), alloxanthin (cryptophytes; 2–4%) and lutein–zeaxanthin (chlorophytes–cyanobacteria; 10–13%) comprised lesser amounts. Pigments in unfertilized mesocosms were not significantly different from those in lake samples (*t*-test, $p > 0.05$, df = 2).

Trout P Excretion

Bioenergetics models estimated that phosphorus excretion by trout in Snowflake Lake increased rapidly after stocking to a peak of 6000 g P·yr^{-1} (13.8 μg·L^{-1}·yr^{-1}) in 1968 when 10 000 fish remained in the lake (Fig. 6). Maximum estimates of annual P supply rate were increased to 17.2 μg·L^{-1}·yr^{-1} by assuming that dead fish remain in the lake and release P to phytoplankton. In both cases, excretion declined to trace levels by 1982, at which time all fish were assumed to have died (Fig. 6). The last recorded brook trout was recovered from Snowflake Lake in 1984. Overall, the rate of P supply was significantly correlated ($r^2 = 0.76$, $p < 0.0001$, $N = 12$) to the concentration of fossil pheophytin *b*, a chlorophyll *b* derivative from chlorophyte algae and higher plants.

Discussion

Reliability of Fossil Chronology

Replicate ^{210}Pb analyses of cores from Harrison Lake were in good agreement (SE = 8.5%) and suggest that analyses from single cores in Pipit and Snowflake lakes were reliable. However, estimates of sediment accumulation rate, and hence depth–age relations, were extremely sensitive to assumptions of background ^{210}Pb activity because of low total activity in the sediments of all three lakes. For example, despite low error surrounding the ^{210}Pb activity – mass accumulation relationship (Fig. 2), estimates of Harrison Lake sediment accumulation increased from 15.0 to 20.5 mg·cm^{-2}·yr^{-1} when background ^{210}Pb was decreased from 6.4 to 5.6 dpm·(g dry wt)$^{-1}$. Consequently, dates assigned to individual depths are tentative, and errors calculated from regressions of ^{210}Pb activity versus sediment mass accumulation are regarded as minimum estimates.

Sediment ages derived from ^{210}Pb and ^{137}Cs analyses differed slightly in Snowflake Lake. The highest pigment concentrations occurred near 1960 ± 5 yrs when based on ^{210}Pb activities, whereas the same peaks occurred near 1968 when calculated using ^{137}Cs (Fig. 6). Similarly, initial increases in fossil pigment concentration occurred shortly after 1954 ± 2 yr according to ^{137}Cs dating, and 1947 ± 7 yr based on ^{210}Pb activity. Overall, ^{210}Pb analysis overestimated sediment age relative to ^{137}Cs dates, and suggested that pigment increases began slightly prior to trout introduction in Snowflake Lake (1960).

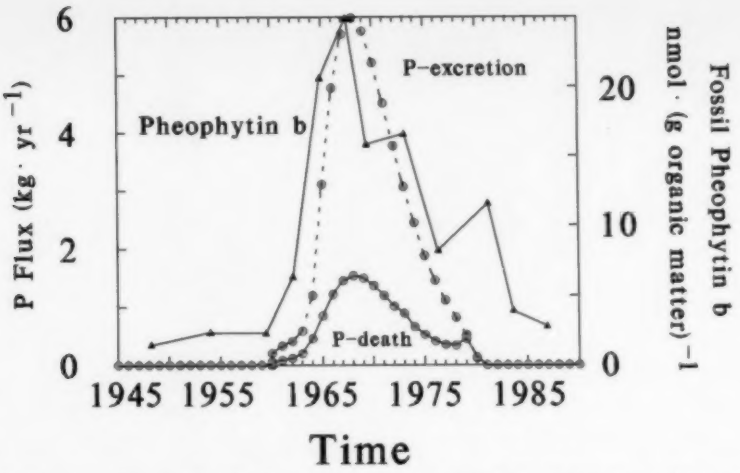

FIG. 6. Concentrations of fossil pheophytin *b* from chlorophytes (triangles, solid line) and estimated P supply from trout excretion (circles, hatched line) or death and decomposition (circles, solid line) in Snowflake Lake, ca 1945–90. Fossil dates are based on ^{137}Cs analysis.

Some fossil stratigraphies may have been subject to minor post-depositional sediment mixing. ^{210}Pb activity declined exponentially with sediment depth in Pipit Lake, but not in Harrison Lake or Snowflake Lake where activities in the upper 3.5 cm were similar (Fig. 3). Constant ^{210}Pb activity in surface sediments often indicates sediment perturbation or post-depositional ^{210}Pb migration (Oldfield and Appleby 1984). Such sediment mixing both broadens stratigraphic peaks (Robbins 1982; Miller and Heit 1986) and moves maxima deeper in the sediments (Davis 1974), but does not reduce the interpretability of strong fossil signals (i.e., peak/baseline ≥ 5; Leavitt and Carpenter 1989). Mild sediment mixing is consistent with the absence of laminae, the lack of distinct 1963 peaks in ^{137}Cs activity, and the presence of chironomids in near-surface sediments in Snowflake Lake. Such sediment mixing may partly explain why fossil pigment concentrations apparently increased prior to trout introduction in Snowflake Lake (1960; Fig. 4a), but not Pipit Lake (1964; Fig. 4b).

Algal Biomass in Stocked Alpine Lakes

Comparison of fossil profiles from stocked Snowflake and Pipit lakes with those from unstocked Harrison Lake suggests that algal biomass increased 4- to 10-fold coincident with trout introduction (Fig. 4). Overall, phytoplankton community response to trout stocks was similar in Snowflake and Pipit lakes and between fossil pigments. In both stocked lakes, all fossil pigment increases were statistically significant ($p < 0.05$), whereas the pigment increases in unstocked Harrison Lake were usually nonsignificant (Table 5). Several mechanisms may have led to increased algal biomass including increased nutrient supply from allochthonous sources, increased nutrient cycling within the food web, elimination of grazing by large herbivores, and increased production by benthic algae. These mechanisms are not mutually exclusive, and we evaluate the plausibility of each below.

Allochthonous fertilization

Fertilization of Snowflake and Pipit lakes by allochthonous sources is unlikely to have stimulated algal production during the 1960s. There have been no local fires since ca 1925 (Beder 1967), and these alpine lakes were over 1 km distant from the closest source of physical disturbance, a road that lies at 200 m lower elevation. We also infer that regional changes in precipitation did not increase algal biomass because all three lakes lie within 8 km of each other, and are at a similar altitude and exposure (Table 1), yet only Snowflake and Pipit lakes have statistically significant increases in fossil pigments since the early 1960s. While high concentrations of fossil pigments were also recorded in the uppermost sediments of Harrison Lake (Fig. 4c), these patterns were not significant ($p > 0.05$), and are similar to those produced by pigment diagenesis immediately after deposition (Hurley and Armstrong 1990, 1991; Leavitt 1993).

Nutrient cycling

Bioenergetics models estimated that stocked trout could supply over 13.8 $\mu g\ P \cdot L^{-1} \cdot yr^{-1}$ to phytoplankton in Snowflake Lake and that changes in P flux were correlated ($r^2 = 0.76$, $p < 0.0001$) to algal biomass, as measured by fossil pheophytin *b* (Fig. 6). Our mesocosm experiments showed that algal communities in Snowflake Lake were very sensitive to small changes in nutrient supply (Fig. 5). The ability of fish to increase algal standing crop and change community composition by excretion of soluble nutrients has been previously demonstrated using mesocosms (Reinertsen et al. 1986; Vanni and Findlay 1990; Schindler 1992). Nutrient recycling to algae from fish may be particularly important when fishes feed on benthic organisms (as in Snowflake Lake; Anderson and Donald 1978) and provide a direct link between benthic and pelagic nutrient pools (Brabrand et al. 1990; Havens et al. 1993; Schindler et al. 1993).

Herbivory

Introduction of planktivorous trout to fishless Snowflake and Pipit lakes caused extirpation of large herbivores (*Daphnia*) and omnivores (*Gammarus*) (Anderson 1972, 1975). Elimination of large, effective grazers should allow edible algae to flourish (Carpenter et al. 1987). Elser and Goldman (1990, 1991) have shown that *Daphnia* dramatically reduce

edible algae in Lake Tahoe, an unproductive subalpine lake. In contrast, grazing by the dominant native zooplankton (*Diaptomus tyrelli*) had little effect on the phytoplankton community of small diatoms and cryptophytes (Elser and Goldman 1991; Hunter et al. 1990). Neill (1988) also found that grazing by *Daphnia* helped regulate food-web structure in montane lakes by reducing algal and rotifer densities.

In general, fossil pigment profiles only partly support the hypothesis that herbivores are important regulators of algal biomass in alpine lakes. As predicted, fossil pigments from edible chlorophytes and cryptophytes increased concomitant with or shortly after stocking (Fig. 4a, b). Coeval historical records of Anderson confirm our paleoecological interpretation and show that chlorophytes and cryptophytes accounted for up to 75% of the algal biomass (as volume) in Snowflake Lake during summers between 1969 and 1977 (Anderson 1974b; Anderson and Donald 1978).

Not all aspects of the fossil record were consistent with reduced herbivory after trout introduction. For example, the grazing indicator, pheophorbide *a*, increased parallel to other pigments concomitant with stocking (Fig. 4a, b). Pheophorbide *a* is produced from chlorophyll *a* in the digestive tract of herbivorous zooplankton (Daley 1973; Carpenter and Bergquist 1985). Therefore, increased fossil pheophorbide *a* concentrations suggest that total algal ingestion increased after *Diaptomus tyrelli* and rotifers replaced *Daphnia* and *Gammarus* (Anderson 1972, 1974a; Anderson and Donald 1978). Unfortunately, interpretation of this signal is complicated because the mass-specific rate of pheophorbide *a* production is greater for rotifers than for *Daphnia* (Carpenter and Bergquist 1985). In addition, deepwater copepods may transport pheophorbide to sediments more efficiently than *Daphnia* in unstratified lakes (Carpenter et al. 1988; Kitchell and Carpenter 1987). Field experiments will be required to resolve the exact meaning of pheophorbide and the importance of herbivory by *Daphnia* in these alpine systems.

Benthic production

Trout may have indirectly increased the standing crop of benthic algae by eliminating omnivorous *Gammarus lacustris* (Anderson 1972; Anderson and Raasveldt 1974). Analysis of gut contents in 1992 shows that *Gammarus* is partly herbivorous and selectively harvests chlorophytes (P.R. Leavitt, unpublished data). However, we infer that benthic production did not account for the entire increase in algal biomass, because cryptophytes that lack a benthic phase also increased greatly after fish were stocked (Fig. 4).

Conclusions

Six of Canada's western mountain parks have been designated World Heritage Sites, yet over 20% (305) of the park lakes have been altered through introduction of nonnative fish (Donald 1987). Similarly, fewer than 45% of the over 16 000 high mountain lakes in the western United states remain unstocked, although 95% were naturally fishless (Bahls 1992). These introduced trout often reconfigured alpine food webs by eliminating large-bodied invertebrates (Donald 1987). Recovery of stocked lakes is now a priority for national parks management in North America (Mayhood 1992; Bahls 1992).

Our fossil pigment analyses suggest that algal biomass increased 4- to 10-fold after the introduction of trout. These changes may impact the ability of invertebrates to recolonize ultra-oligotrophic alpine lakes. Small changes in algal abundance can alter the relative success of competing invertebrates and, in turn, the species composition of food webs (Neill and Peacock 1980; Neill 1988). Anderson (1974a, 1980) surveyed 340 stocked and natural Rocky Mountain lakes and postulated that increased predation by cyclopoid copepods (*Cyclops, Diacyclops*) after trout introduction may prevent the re-establishment of *Hesperodiaptomus* spp. after trout stocks fail. Because both cyclopoids and *Hesperodiaptomus* are carnivorous in later instars, yet reproduce at different times during the year (Anderson 1970; Anderson 1972; D.W. Schindler, unpublished data), small changes in algal production may strongly influence the success of invertebrate colonization. Ongoing mesocosm experiments are being conducted to investigate the relationship between algal production and invertebrate community structure in these alpine lakes.

Acknowledgments

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Crustacean Zooplankton Communities and Lake Morphometry in Precambrian Shield Lakes

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Keller, W., and M. Conlon. 1994. Crustacean zooplankton communities and lake morphometry in Precambrian Shield lakes. Can. J. Fish. Aquat. Sci. 51: 2424–2434.

To investigate relationships between crustacean zooplankton communities and lake morphometry we sampled 60 near-neutral Precambrian Shield lakes, including many small, shallow lakes. Morphometry-related patterns in the distributions of many zooplankton species were evident. Lake depth determined the occurrence of hypolimnetic species, and lake depth, lake area, and watershed area were positively related to the species richness of zooplankton communities. Among lakes with fish, deeper (maximum depth >8 m) lakes were characterized by greater species richness, higher abundances of a number of species including *Daphnia pulex*, *Daphnia galeata mendotae*, *Daphnia dubia*, and *Diacyclops bicuspidatus thomasi*, and lower abundances of *Leptodiaptomus minutus*, than shallower (maximum depth <8 m) lakes. Increased predation pressure by small fish species in smaller, shallower lakes probably influenced the observed species distributions. Lakes inferred to be fishless based on the presence of *Chaoborus americanus* typically had relatively high abundances of *D. pulex*, *Diaphanosoma brachyurum*, and *Aglaodiaptomus leptopus*, and absences of *D. g. mendotae* and *D. birgei*, patterns attributable to intense invertebrate predation on zooplankton.

Pour étudier les liens existants entre les communautés de crustacés zooplanctoniques et la morphométrie lacustre, nous avons échantillonné 60 lacs pratiquement neutres du bouclier précambrien, y compris de nombreux lacs peu profonds de faible superficie. Les profils liés à la morphométrie étaient évidents dans les distributions de nombreuses espèces de zooplancton. La profondeur du lac déterminait la présence d'espèces hypolimniques et la profondeur et la superficie du lac ainsi que le bassin versant étaient positivement liés à la richesse en espèces des communautés zooplanctoniques. Parmi les lacs poissonneux, les lacs plus profonds (profondeur maximale >8 m) étaient caractérisés par une plus grande richesse en espèces, un plus grand nombre d'espèces, y compris *Daphnia pulex*, *Daphnia galeata mendotae*, *Daphnia dubia* et *Diacyclops bicuspidatus thomasi*, et une plus faible abondance de *Leptodiaptomus minutus* que les lacs moins profonds (profondeur maximale <8 m). La pression accrue de la prédation par les petites espèces de poissons dans les lacs plus petits et moins profonds a probablement influé sur les distributions d'espèces observées. De manière caractéristique, les lacs que l'on supposait non poissonneux en raison de la présence de *Chaoborus americanus* montraient une abondance relativement élevée de *D. pulex*, de *Diaphanosoma brachyurum* et de *Aglaodiaptomus leptopus* ainsi qu'une absence de *D. g. mendotae* et de *D. birgei*, des profils qui sont attribuables à la prédation intense des invertébrés sur le zooplancton.

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A number of surveys investigating relationships between crustacean zooplankton communities and physicochemical lake characteristics have been conducted in North America. Relationships have been established between zooplankton communities and lake acidity (e.g., Sprules 1975; Confer et al. 1983; Brezonik et al. 1984; Keller and Pitblado 1984), glacial history (e.g., Carter et al. 1980; Roff et al. 1981; Keller and Pitblado 1989), and general lake trophic status (e.g., Sprules 1977; Keller and Pitblado 1984). However, clear associations between lake morphometry and zooplankton community structure have not emerged from these studies. While lake morphometry has sometimes been implicated as a factor affecting zooplankton communities (Patalas 1971; Sprules 1977), assessment of effects has been complicated by relationships between lake morphometry and variables such as lake acidity (Sprules 1975; Confer et al. 1983) or water clarity (Patalas 1971; Sprules 1977). There are also differing results reported in the literature. Most studies have reported increased crustacean species richness in larger water bodies (e.g., Patalas 1971; Fryer 1985; Dodson 1991); however, others did not show this pattern (Keller 1981; Keller and Yan 1991). Regional effects may also be important, because some species appear to show differing environmental preferences in different regions (Patalas 1971; Sprules 1977).

There are several lines of reasoning that suggest that zooplankton communities in smaller, shallower lakes may be influenced by somewhat different sets of biological and physical factors than those operating in larger, deeper lakes, which could lead to different zooplankton community characteristics.

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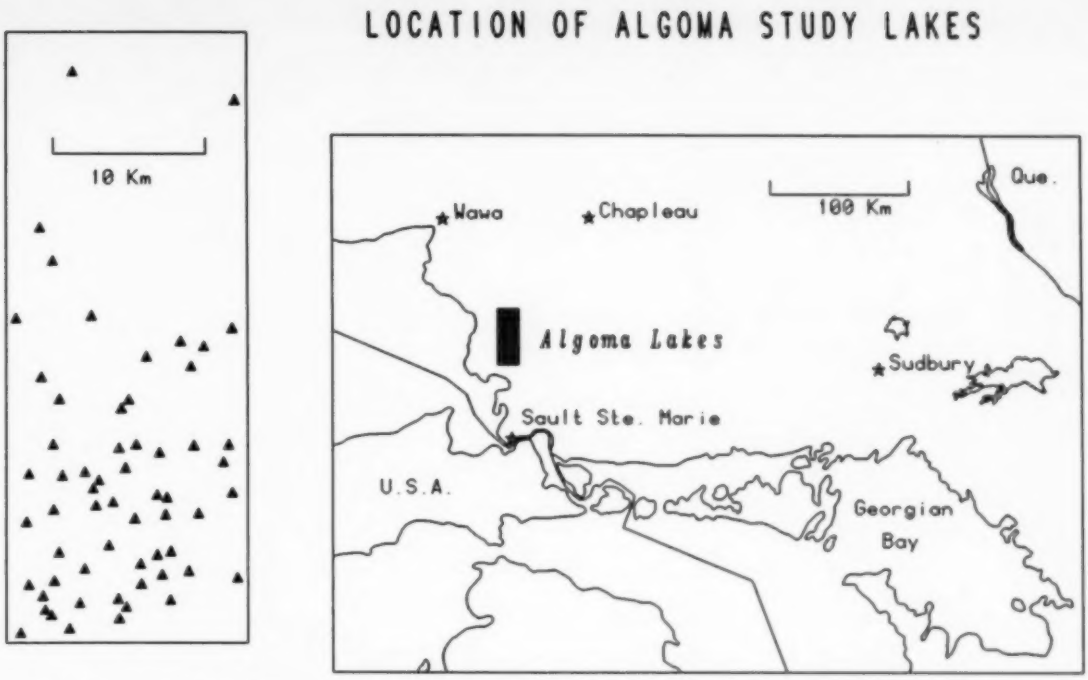

FIG. 1. Locations of the Algoma study area (shaded rectangle) and the sixty study lakes within the area (at left).

Habitat limitations and opportunities for dispersal may influence zooplankton communities. A physically "smaller" environment may reduce opportunities for spatial separation of species and, thus, induce greater competitive interaction. In general, when resources are limiting, large species would be expected to be superior competitors to smaller species, although this pattern is not universal (e.g., DeMott and Kerfoot 1982; Vanni 1986; Bengtsson 1987). Increased homogeneity of the environment in small, shallow lakes could lead to low zooplankton species richness. For example, suitable habitats for cold stenotherms may be limited or absent in shallow lakes. Small lakes are also often headwater lakes with small watersheds. Owing to limited dispersal opportunities or abilities, some zooplankton species may not be able to colonize these waters. In contrast, the proximity of open lake waters to the lake shoreline in small lakes may allow normally littoral species to expand into the limnetic plankton. As well, the very shallow nature of many very small lakes may offer an essentially littoral rather than pelagic habitat.

Factors related to predation may also be important influences on zooplankton communities. In small lakes, a greater proportion of the lake zooplankton may be accessible to fish species that are normally associated with the shoreline areas. Additionally, in small, shallow lakes an increased proportion of the fish species assemblage may be comprised of small planktivorous species, including many cyprinids (Matuszek et al. 1988, 1990). Conversely, because very small, shallow lakes typically have fewer fish species than larger lakes (Matuszek et al. 1988) and may sometimes be naturally devoid of fish (McNicol et al. 1987; Kelso et al. 1992), direct predation on zooplankton by fish could be reduced. In fishless lakes, however, the abundance of predaceous invertebrates, which are normally controlled by fish predation, may be high (Ericksson et al. 1980; McNicol et al. 1987) and may influence zooplankton communities. One such invertebrate predator, *Chaoborus*, can greatly affect the abundance of crustacean zooplankton (Yan et al. 1982; 1991; Nyberg 1984) and is capable of virtually eliminating some zooplankton species (von Ende and Dempsey 1981; Vanni 1988).

Previous zooplankton surveys in Precambrian Shield lakes have not specifically examined lake morphometry as a factor directly or indirectly affecting zooplankton communities. In addition to the confounding influence of other variables that may be correlated with lake morphometry, a problem with many previous surveys is simply that very small lakes, where morphometry-related mechanisms are expected to be most operative, have been largely excluded. Past large-scale zooplankton surveys (e.g., Carter et al. 1980, 1986; Keller and Pitblado 1989) have been strongly biased towards larger lakes. For example, the minimum lake sizes sampled in the extensive surveys of Keller and Pitblado (1989) were 23 ha for northeastern Ontario (n = 161) and 90 ha for northwestern Ontario (n = 137). Patalas (1971) did examine a number of small, shallow lakes in his survey of 45 northwestern Ontario lakes. However, while patterns related to lake morphometry were described in that study, possible underlying mechanisms were not examined.

In this study we examine the species richness and species composition of midsummer crustacean zooplankton communities in 60 lakes, including many small, shallow lakes, in the Algoma area of Ontario. The purpose is to define empirical relationships between lake morphometry and crustacean zooplankton communities, and determine if any of the potential controlling mechanisms outlined above can be

TABLE 1. Summary of chemical and physical characteristics of the Algoma study lakes (n = 60).

Variable	Mean	Median	Range
Lake maximum depth (m)[a]	7.5	6.2	0.8–20.0
Lake area (ha)	30.0	14.4	1.8–175.0
Watershed area (ha)[b]	587	165	28–2805
Secchi depth (m)[c]	3.9	3.6	0.8–10.5
Dissolved organic carbon ($mg \cdot L^{-1}$)	4.7	4.2	2.1–13.0
Total phosphorus ($\mu g \cdot L^{-1}$)	7.1	7.0	1.1–17.0
Chlorophyll *a* ($\mu g \cdot L^{-1}$)	2.8	2.4	0.6–15.1
pH	6.6	6.8	6.0–7.4
Conductivity ($\mu S \cdot cm^{-1}$)	28.1	28.5	17.0–44.0
Calcium ($mg \cdot L^{-1}$)	3.6	3.5	1.2–7.6
Aluminum ($\mu g \cdot L^{-1}$)	65	54	10–210

[a]Depth at sampling locations; assumed to be maximum depth.
[b]Does not include lake area.
[c]Secchi disc visible to bottom in some shallow lakes.

supported by field data. The overall objective of this work was to examine the question: how are crustacean zooplankton communities in Precambrian Shield lakes related to lake morphometry? This question is relevant to the water resources of Canada. For example, of the ~227 000 lakes in the province of Ontario, ~135 000 are under 10 ha in area (Cox 1978). Such small lakes, where morphometry-related influences on zooplankton communities may be most important, represent a vast but poorly understood, aquatic resource.

Study Lakes

The 60 study lakes examined are part of a larger lake set sampled by Pitblado (1987). To minimize confounding influences on community structure associated with lake acidity, only lakes with pH >6.0, the apparent threshold for significant acidification-related biological damage (RMCC 1990) were considered. The effects of acidification on zooplankton communities are well documented (e.g., Sprules 1975; Keller and Pitblado 1984; Havens et al. 1993). The lakes are located within a 600-km^2 rectangular area, 70 km north of Sault Ste. Marie, in the Algoma region of Ontario (Fig. 1). In this area of the Precambrian Shield, the bedrock is comprised predominantly of metavolcanics, metasediments, and granitic rocks of Archean age. Overburden throughout this area is typically thin, discontinuous and sandy, and is associated with a ground moraine (Fortescue and Stahl 1987).

As a group, the study lakes can be considered as relatively small (median area 14.4 ha), shallow (median maximum depth 6.2 m), dilute (median conductivity 28.5 $\mu S \cdot cm^{-1}$), and nutrient poor (median total phosphorus (TP) 7 $\mu g \cdot L^{-1}$), although substantial variation in these general characteristics does occur (Table 1). Complete listings of physicochemical data are provided in Pitblado (1987).

Unfortunately, the fish communities existing in these specific lakes are not known. However, assessment of fish communities in other lakes in the same general area (Kelso et al. 1982) has shown that lake trout (*Salvelinus namaycush*) and brook trout (*Salvelinus fontinalis*) are the common gamefish species in this region, and that these gamefish species are commonly associated with populations of white sucker (*Catostomus commersoni*). Nongamefish communities are expected to resemble those reported for small (1.4–23.1 ha) lakes in the Ranger Lake area, 40 km to the southeast (Bendell and McNicol 1987). Bendell and McNicol (1987) reported a variety of cyprinid species from the Ranger Lake area, particularly northern redbelly dace (*Phoxinus eos*), finescale dace (*Phoxinus neogaeus*), pearl dace (*Semotilus margarita*), fathead minnow (*Pimephales promelas*), common shiner (*Notropis cornutus*), creek chub (*Semotilus atromaculatus*), and blacknose dace (*Rhinichthys atratulus*). Non-cyprinid species captured in that study included white sucker, brook stickleback (*Culaea inconstans*), Iowa darter (*Etheostoma exile*), and brook trout.

Methods

Each of the study lakes was sampled at an open-water location, once during the period August 19–24, 1986. While single samples do not account for spatial or temporal variations in zooplankton communities, single sample surveys have provided much valuable information on zooplankton in Precambrian Shield lakes (e.g., Patalas 1971; Sprules 1975). The sampling location was assumed to approximate the point of maximum lake depth because of its relatively central position. Where depth was sufficient, zooplankton samples were collected as single vertical hauls from 1 m above bottom to the lake surface with a nonmetered, 80-μm mesh, 12.5-cm mouth-diameter net. In very shallow lakes (<4 m), horizontal tows over a distance of 10–20 m were taken.

Samples were immediately preserved with 5% buffered formalin. Identification and enumeration procedures followed those outlined in Yan and Strus (1980). Taxonomic references included Brooks (1959), Wilson (1959), Yeatman (1959), and Deevey and Deevey (1971). Animals identified as *Daphnia catawba* were considered to be *D. pulex* after Dodson (1981). Cladocera and adult copepods were identified to species, while copepod nauplii and copepodids were only identified to suborder.

Physical and chemical information on the lakes was obtained from Pitblado (1987). Single water chemistry samples were collected from the same locations, at the same times, as zooplankton samples. Collection and analytical techniques for water chemistry samples are outlined in Pitblado (1987) and MOE (1981), respectively.

Prior to parametric statistical analyses, the distributions of data were examined, and $\log_{10}$ transformations were applied

where necessary to normalize the data and stabilize the variance. Transformed data were re-examined, and if necessary to achieve normality in the data distributions, outliers (>3 standard deviations from the mean) were set to values just slightly higher than the highest value in the rest of the data set, a variation of "winsorizing" (Sokal and Rohlf 1981). Normality of untransformed and transformed data was assessed by examination of frequency distribution histograms and normal probability plots, and by testing for significant ($p < 0.05$) departures from a normal distribution based on a Kolmogorov–Smirnov test.

Principal components analysis (PCA) of $\log_{10}(x + 1)$ transformed data was chosen as a primary method of analyzing patterns in species abundances, given the many past demonstrations of the usefulness of this general technique for revealing patterns in zooplankton community composition (Sprules 1977; Roff et al. 1981; Carter et al. 1986; Keller and Pitblado 1989). Additional statistical techniques used for data analyses included Pearson correlation analyses; stepwise multiple linear regression; examination of characteristics within, and differences between, defined lake groups using box plots depicting medians, ranges, and upper and lower quartiles; and nonparametric Kruskal–Wallis one-way analysis of variance (ANOVA). If significant ($p < 0.05$) differences among groups existed, differences between groups were determined by a pairwise Wilcoxon Mann–Whitney U nonparametric test. Statistical analyses were conducted using SPSS/PC+ (SPSS Inc. 1990).

Results

General Occurrence of Species

A total of 28 crustacean plankton species was identified from the collections (Table 2). All the species listed in Table 2 have previously been reported from Ontario (Patalas 1971; Brandlova et al. 1972; Carter et al. 1980; Keller and Pitblado 1989). Five of these species can be generally regarded as hypolimnetic forms (*Cyclops scutifer, Leptodiaptomus sicilis, Senecella calanoides, Eubosmina longispina*, and *Daphnia longiremis*), while *Orthocyclops modestus* and *Sida crystallina*, although they are reported from the limnetic plankton, are probably mainly littoral species (Ward and Whipple 1959; Carter et al. 1980).

Bosmina longirostris, Leptodiaptomus minutus, Mesocyclops edax, Tropocyclops extensus, Holopedium gibberum, and *Daphnia pulex* were the most common species, occurring in over 50% of the lakes. *Diaphanosoma birgei, Diaphanosoma brachyurum, Epischura lacustris, Skistodiaptomus oregonensis, Daphnia galeata mendotae, Daphnia dubia, Diacyclops bicuspidatus thomasi*, and *Aglaodiaptomus leptopus* were collected from 25 to 50% of the lakes. The remaining species were collected from <25% of the lakes.

Lake maximum depth was the best correlate with species richness, defined as the total number of species collected from each lake ($r = 0.33$; $p < 0.05$). Lake depth, however, was correlated ($p < 0.05$) positively with lake area, watershed area, and Secchi transparency ($r = 0.37$–0.78) and negatively with dissolved organic carbon (DOC), TP, and Al ($r = -0.49$ to -0.58) (Table 3). Lake area ($r = 0.25$) and watershed area ($r = 0.27$) were also correlated positively ($p < 0.05$) with species richness. However, lake depth was the only environmental correlate with species richness selected by a stepwise multiple linear regression; other environmental variables did not explain a significant amount of the residual variation in species richness. Visual examination of patterns (Fig. 2) confirmed that species richness was highest in the deeper lakes, and showed evidence of a decline commencing at about 8 m, followed by an increase in the shallowest (<2 m) lakes. This general trend was less pronounced, but remained evident when hypolimnetic species were excluded from the analysis.

TABLE 2. Percent occurrence of crustacean zooplankton species in the Algoma study lakes ($n = 60$).

Species	% occurrence
Bosmina longirostris	92
Leptodiaptomus minutus	92
Mesocyclops edax	88
Tropocyclops extensus	88
Holopedium gibberum	68
Daphnia pulex	52
Diaphanosoma birgei	50
Diaphanosoma brachyurum	50
Epischura lacustris	42
Skistodiaptomus oregonensis	42
Daphnia galeata mendotae	40
Daphnia dubia	30
Diacyclops bicuspidatus thomasi	27
Aglaodiaptomus leptopus	27
Daphnia longiremis	17
Eubosmina longispina	17
Daphnia retrocurva	15
Orthocyclops modestus	15
Eubosmina coregoni	8
Leptodora kindtii	8
Polyphemus pediculus	8
Chydorus sphaericus	7
Senecella calanoides	7
Cyclops scutifer	5
Onychodiaptomus sanguineus	5
Ceriodaphnia sp.	3
Leptodiaptomus sicilis	3
Sida crystallina	3

Principal Components Analysis

Analysis, through PCA, of patterns in abundances for species occurring in >10% of the lakes indicated that a total of 45.4% of the variance in the species abundance data could be explained by the first three components extracted by the analysis (Table 4). Relationships between lake scores on these components are depicted in Fig. 3.

The first component (PC1), explaining 19.3% of the variance in the species abundance data, was characterized by relatively high positive loadings of a number of the most common species including *T. extensus, H. gibberum, M. edax*, and *B. longirostris*. These species apparently were not greatly restricted by the range in environmental characteristics of the study lakes. The only significant ($p < 0.05$) environmental correlate with PC1 was chlorophyll *a* (Table 4).

The second component (PC2), explaining 15.9% of the variance in species abundances, was identified by relatively high positive loadings of *D. b. thomasi* and three *Daphnia* species (*D. longiremis, D. dubia*, and *D. g. mendotae*; Table 4). PC2 was characterized by positive ($p < 0.05$) correlations with lake depth, lake area, Secchi transparency, and watershed area, and negative correlations with DOC

TABLE 3. Matrix of Pearson correlation coefficients for relationships between environmental variables, for the Algoma study lakes (n = 60). Variables except pH, TP, and conductivity were log transformed.

	Depth	Area	Watershed	Secchi	DOC	TP	Chl *a*	pH	Cond.	Ca	Al
Max. depth											
Area	0.61[a]										
Watershed	0.37[a]	0.82[a]									
Secchi	0.78[a]	0.61[a]	0.38[a]								
DOC	−0.58[a]	−0.49[a]	−0.28[a]	−0.83[a]							
TP	−0.49[a]	−0.45[a]	−0.26[a]	−0.67[a]	0.60[a]						
Chl *a*	−0.07	−0.15	−0.15	−0.31[a]	0.16	0.49[a]					
pH	0.12	−0.29[a]	0.28[a]	0.12	−0.13	−0.09	0.14				
Cond.	−0.17	−0.11	−0.01	−0.33[a]	0.34[a]	0.27[a]	0.22[a]	0.76[a]			
Ca	−0.17	−0.13	−0.03	−0.36[a]	0.39[a]	0.26[a]	0.17	0.77[a]	0.96[a]		
Al	−0.49[a]	−0.34[a]	−0.10	−0.61[a]	0.63[a]	0.46[a]	0.02	−0.47[a]	−0.20	−0.13	
C. americanus	−0.05	−0.27[a]	−0.36[a]	0.05	−0.12	−0.12	−0.31[a]	−0.33[a]	−0.27[a]	−0.26[a]	0.15

[a] $p < 0.05$.

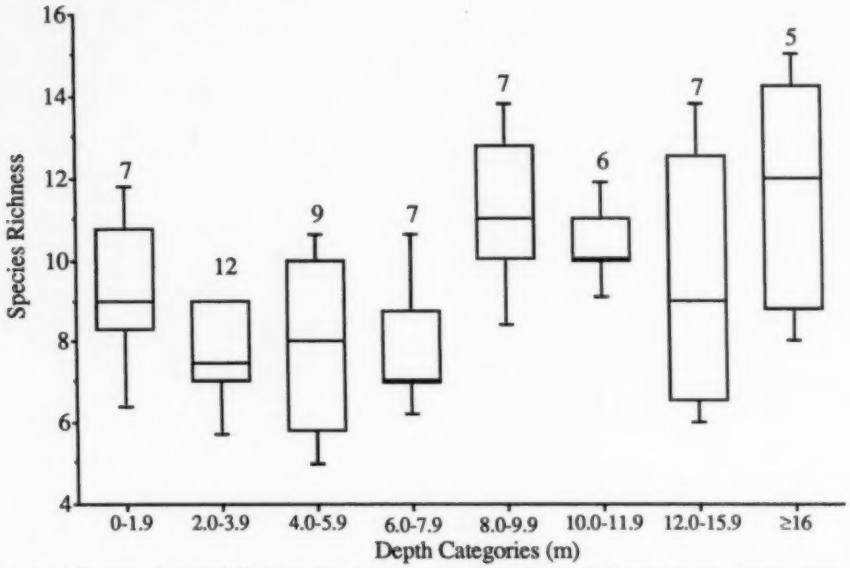

FIG. 2. Patterns in zooplankton species richness across lake depth categories in the Algoma study lakes. The horizontal line is the median, the box encompasses 50% of the values, and the error bars give the range in the data. Numbers above each boxplot indicate n.

and *C. americanus* abundance (Table 4). These variables were intercorrelated (Table 3).

The third component (PC3), explaining 10.2% of the variance in the species abundance data, was identified by high positive loadings of *A. leptopus*, *D. brachyurum*, and *L. minutus* (Table 4). Lake area, pH, Ca, conductivity, and watershed area were negatively correlated ($p < 0.05$) with PC3, while *C. americanus* abundance was positively correlated with PC3 (Table 4).

A fourth component extracted by the analysis explained an additional 9.1% of the variance in the species-abundance data and was characterized by high positive loadings of *O. modestus* and *D. pulex*; however, this component was not correlated with any of the environmental variables measured.

Differences between Lake Groups

Zooplankton species occurrences and abundances were examined in three lake groups. Lakes containing larval *C. americanus*, a predaceous dipteran characteristic of lakes without fish (Pope et al. 1973; von Ende 1979) were classified as fishless. The remaining lakes, presumed to contain fish, were divided into two depth groups (shallower, <8 m; deeper, >8 m). The division into these depth categories was based on the evidence of a discontinuity in species richness at ~8 m (Fig. 2). These depth categories also served to roughly divide lakes among those expected to be dominated by smaller and larger fish species, and those expected to show some thermal stratification or no stratification (W. Keller, personal observations).

A number of species showed differences in relative occurrence between these lake groups (Table 5). Considering only zooplankton species that showed at least a 10% difference in occurrence between the two lake depth groups, *D. pulex*, *D. brachyurum*, *D. g. mendotae*, *D. dubia*, *D. b. thomasi*, *D. longiremis*, *E. longispina*, *Leptodora kindtii*, *S. calanoides*, *M. edax*, *P. pediculus*, and *C. scutifer* were more common among deeper lakes, while *L. minutus*, *H. gibberum*, *D. birgei*, and *A. leptopus* had increased occurrence among

TABLE 4. Varimax rotated factor matrix of zooplankton species abundances with the first four principal components, for the Algoma study lakes. Only species occurring in >10% of the lakes are considered. For full species names see Table 2.

Taxa	Principal component[a]			
	PC1	PC2	PC3	PC4
T. extensus	0.86[b]	−0.02	0.04	0.10
H. gibberum	0.75[b]	−0.15	0.06	0.25
M. edax	0.68[b]	0.10	0.31	−0.11
Cyclopoid copepodids	0.68[b]	0.45	0.08	0.25
B. longirostris	0.55[b]	−0.13	−0.19	0.05
D. b. thomasi	−0.01	0.89[b]	−0.05	0.30
D. longiremis	−0.09	0.76[b]	−0.05	0.04
D. dubia	0.15	0.71[b]	−0.07	0.00
D. g. mendotae	−0.02	0.65[b]	−0.18	−0.12
A. leptopus	−0.03	−0.16	0.90[b]	0.17
D. brachyurum	0.39	−0.05	0.80[b]	−0.08
L. minutus	0.05	−0.13	0.68[b]	−0.15
O. modestus	0.04	−0.05	0.01	0.85[b]
Cyclopoid nauplii	0.37	0.14	−0.03	0.78[b]
D. pulex	0.00	−0.13	0.08	0.51[b]
D. birgei	0.18	−0.07	−0.13	0.17
E. lacustris	0.08	0.04	−0.09	0.20
D. retrocurva	0.27	−0.03	−0.06	−0.09
Calanoid copepodids	0.08	0.30	0.10	−0.26
E. longispina	−0.05	0.24	−0.13	−0.13
S. oregonensis	0.29	−0.08	−0.14	0.10
Calanoid nauplii	−0.30	−0.20	0.26	−0.22
Eigenvalue	4.24	3.50	2.25	2.01
% variance explained	19.3	15.9	10.2	9.1
Cumulative percent	19.3	35.2	45.4	54.6

[a]Environmental variables with significant (Pearson r, $p < 0.05$) correlations with principal component factor scores were: PC1, chlorophyll a ($r = 0.33$); PC2, lake depth ($r = 0.42$), watershed area ($r = 0.34$), lake area ($r = 0.31$), Secchi (0.29), *C. americanus* ($r = -0.26$), DOC ($r = -0.25$); PC3, *C. americanus* ($r = 0.43$), Ca ($r = -0.35$), conductivity ($r = -0.34$), pH ($r = -0.33$), watershed area ($r = -0.33$), lake area ($r = -0.22$). There were no significant ($p < 0.05$) environmental correlates with PC4.

[b]Loading > 0.5; loadings are correlations between species and components after orthogonal rotation.

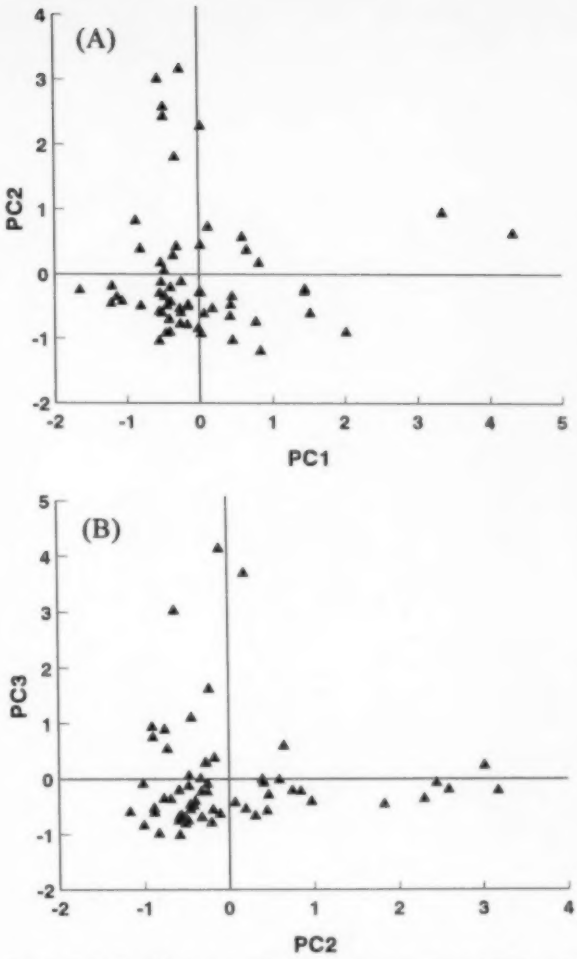

FIG. 3. Relationship between lake factor scores for (a) PC1 and PC2 and (b) PC2 and PC3 for the Algoma study lakes.

shallower lakes (Table 5). Considering abundance, *L. minutus* had higher abundance ($p < 0.05$) in shallower lakes, while a number of species, including *D. pulex*, *D. g. mendotae*, *D. dubia*, and *D. b. thomasi*, as well as several hypolimnetic species, had higher abundances in deeper lakes (Table 6). The environmental variables dissolved organic carbon (DOC), Al, and total phosphorus (TP) were higher ($p < 0.05$) in concentration in shallower lakes, while lake area, watershed area, and Secchi transparency were lower ($p < 0.05$) (Table 7).

Lakes inferred to be fishless based on the presence of *C. americanus* had the highest percent occurrences of *T. extensus*, *D. pulex*, *D. brachyurum*, *A. leptopus*, *O. modestus*, *H. gibberum*, and *S. crystallina*, and conspicuous absences of *D. birgei*, *D. b. thomasi*, *D. g. mendotae*, and hypolimnetic species (Table 5). They differed from shallower lakes by having higher ($p < 0.05$) abundances of *D. pulex*, *D. brachyurum*,, *S. crystallina*, and *A. leptopus* and an absence of *D. birgei*. Fishless lakes also had higher abundances of a number of species, particulary *A. leptopus*, *S. crystallina*, and *D. brachyurum*, and lower abundances of *D. dubia*, than deeper lakes (Table 6). Fishless lakes had lower ($p < 0.05$) chlorophyll *a*, watershed area, and pH than shallower lakes. They had lower ($p < 0.05$) depth, lake area, watershed area, and pH than deeper lakes (Table 7).

Species richness was lower ($p < 0.05$) in shallower lakes and fishless lakes than in deeper lakes. There was no difference ($p > 0.05$) in species richness between shallower lakes and fishless lakes.

Discussion

Overall, the Algoma study lakes contained a zooplankton species assemblage (Table 2) that was similar to lakes in other regions of Ontario. Of the 28 species present in the Algoma lakes, 26 species occurred in surveys of 161 lakes in northeastern Ontario and 137 lakes in northwestern Ontario (Keller and Pitblado 1989; lakes with pH > 6.0 only). The total number of species collected in the Algoma lakes (28) was slightly lower than the total numbers of species collected by Keller and Pitblado (1989) in surveys of northeastern

TABLE 5. Percent occurrence of crustacean zooplankton species within groups of "deep" (>8 m), "shallow" (<8 m), and "fishless" (1.4 to 12.2 m) lakes for the Algoma study lakes. Deep and shallow lakes contain fish. Absence of fish was inferred from the presence of *C. americanus*. For full species names see Table 2.

Species	"Deep" lakes (with fish) (n = 22)	"Shallow" lakes (with fish) (n = 29)	"Fishless" lakes (n = 9)
B. longirostris	91	93	89
L. minutus	86	97	89
M. edax	100	79	89
T. extensus	82	90	100
H. gibberum	59	72	78
D. pulex	68	31	78
D. birgei	50	66	0
D. brachyurum	55	31	100
E. lacustris	50	41	22
S. oregonensis	45	41	33
D. g. mendotae	77	24	0
D. dubia	50	21	11
D. b. thomasi	55	14	0
A. leptopus	9	21	89
D. longiremis	36	7	0
E. longispina	36	7	0
D. retrocurva	18	14	11
O. modestus	14	10	33
E. coregoni	9	7	11
L. kindtii	18	3	0
P. pediculus	14	3	11
C. sphaericus	5	10	0
S. calanoides	18	0	0
O. sanguineus	9	0	11
C. scutifer	14	0	0
Ceriodaphnia sp.	0	3	11
L. sicilis	9	0	0
S. crystallina	0	0	22

TABLE 6. Zooplankton taxa that showed significant ($p < 0.05$) differences in abundance between "deep" (n = 22), "shallow" (n = 29), and "fishless" (n = 9) lake groups for the Algoma study lakes. Testing employed a nonparametric Kruskal–Wallis one-way ANOVA. If significant ($p < 0.05$) differences among groups existed, differences between groups were determined by Wilcoxon Mann–Whitney U-tests. Deep and shallow lakes contain fish. Absence of fish was inferred from the presence of *C. americanus*. For full species names see Table 2.

	Comparison		
Species	"Deep"–"shallow"	"Deep"–"fishless"	"Shallow"–"fishless"
L. minutus	+		
D. pulex	–		+
D. birgei		–	–
D. brachyurum		+	+
D. g. mendotae	–	–	
D. dubia	–	–	
D. b. thomasi	–	–	
A. leptopus		+	+
D. longiremis	–	–	
E. longispina	–	–	
S. calanoides	–		
S. crystallina		+	+
Calanoid copepodids		–	
Calanoid nauplii	+		–
Cyclopoid copepodids	–	–	

(35 species) and northwestern (36 species) Ontario lakes. However, those surveys contained many more lakes than the Algoma survey, and the additional species recorded were generally rare. These comparisons show no evidence of any unique zoogeographical influence or barrier to species dispersal in the Algoma study area.

Examination of the species richness and species composition of crustacean zooplankton communities in the Algoma lakes did offer evidence that lake morphometry is an important factor influencing zooplankton communities. While the intercorrelations observed between lake depth, lake area, watershed area, TP, Secchi transparency, and DOC (Table 3) make it difficult to separate the independent influences of these variables, the findings that lake depth emerged as the best correlate with species richness, and of the environmental variables measured had the highest correlation with PC2 of the species abundance PCA (Table 4), suggest that lake depth is a key factor.

These results contrast with the results of other surveys spanning very large ranges in lake morphometry, where lake area generally was a slightly better correlate with species richness than lake depth (e.g., Patalas 1971; Dodson 1991, 1992). This suggests that, on a very broad scale, area may be a more important influence, while on a more restricted scale, depth may assume increased importance. Re-analysis of a portion of the data set of Patalas (1971) comprising only lakes of comparable morphometry to the Algoma lakes (area <200 ha; depth <30 m; n = 32) also revealed that depth (r = 0.39) was a better correlate with species richness than area (r = 0.27) while for the entire data set (n = 45) a reverse pattern was reported (area, r = 0.52; depth, r = 0.38; Patalas 1971).

The significant correlations observed between lake and watershed area and species richness are consistent with the principles of the equilibrium theory of island biogeography (MacArthur and Wilson 1967) that identify source populations and island size, in this context lake size or possibly lake volume, as important factors affecting species richness. However, the fact that depth was the best correlate with species richness suggests that richness in these lakes may be more dependent on processes internal to the lake and not external factors like colonization opportunities. For pelagic zooplankton, depth probably represents a simple, but good measure of the habitat type and diversity. Depth is closely linked to other important lake characteristics such as general trophic status, degree of thermal stratification, occurrence and extent of anoxia, and fish community composition. Depth may also provide a good definition of the actual space available to the pelagic zooplankton community because spatial separation, thus potential for coexistence of functionally similar species, may be related to the vertical dimension of the habitat (Rigler and Langford 1967; Makarewicz and Likens 1975). The influences of depth on zooplankton communities may, however, be manifested as both direct and indirect effects.

A primary direct effect of lake depth was the limitation on the occurrence of some zooplankton species with strict thermal requirements. Hypolimnetic species including *D. longiremis*, *C. scutifer*, *L. sicilis*, *E. longispina*, and *S. calanoides*

TABLE 7. Summary of chemical and physical characteristics within "deep" (n = 22), "shallow" (n = 29), and "fishless" (n = 9) lakes. Testing employed a nonparametric Kruskal–Wallis one way ANOVA. If significant ($p < 0.05$) differences among groups existed, differences between groups were determined by Wilcoxon Mann–Whitney U-tests. Deep and shallow lakes contain fish. Absence of fish was inferred from the presence of *C. americanus*.

	"Deep" lakes (>8 m)		"Shallow" lakes (<8 m)		"Fishless" lakes (1.4 to 12.2 m)	
Variable	Mean	Median	Mean	Median	Mean	Median
Max. depth (m)[a,c]	13.0	11.7	3.9	3.7	6.2	4.5
Area (ha)[a,c]	50.2	28.9	16.3	11.5	24.7	4.5
Watershed (ha)[a,b,c]	835	535	468	145	366	56
Secchi (m)[a,d]	5.3	5.3	2.9	2.5	3.9	4.5
DOC ($mg \cdot L^{-1}$)[a]	3.9	3.5	5.3	4.8	4.9	3.9
TP ($\mu g \cdot L^{-1}$)[a]	5.5	5.0	8.7	8.0	6.1	7.0
Chl a ($\mu g \cdot L^{-1}$)[b]	2.5	2.5	3.3	2.6	1.6	1.5
pH[b,c]	6.7	6.8	6.6	6.9	6.3	6.4
Conductivity ($\mu S \cdot cm^{-1}$)	28.7	29.5	29.0	29.0	23.3	20.0
Calcium ($mg \cdot L^{-1}$)	3.7	3.7	3.8	3.7	2.7	2.1
Aluminum ($\mu g \cdot L^{-1}$)[a]	46	38	73	58	87	75

[a]Significant ($p < 0.05$) difference between "deep" and "shallow" lakes.
[b]Significant ($p < 0.05$) difference between "shallow" and "fishless" lakes.
[c]Significant ($p < 0.05$) difference between "deep" and "fishless" lakes.
[d]Secchi disc visible to bottom in some shallow lakes.

were rarely or never collected from lakes <8 m deep, a simple reflection of their general inability to inhabit relatively shallow, warm waters. The exclusion of hypolimnetic species from shallower lakes was associated with an overall decrease in species richness with decreasing lake depth (Fig. 2). Lakes with depth <8 m contained an average of 7.9 species while lakes with depth >8 m contained on average 10.8 species. However, the pattern of decreased species richness with decreasing depth remained evident, although it was less pronounced, even when hypolimnetic species were not considered. Excluding hypolimnetic species, average species richness was 7.7 among shallower (<8 m) lakes and 9.5 among deeper (>8 m) lakes.

Other factors, such as increased fish predation among smaller, shallower lakes, probably play an important role in restricting some species. In general, smaller, shallower lakes are considered to have a higher proportion of small fish species, including cyprinids, in the fish community assemblage than larger lakes that support large, piscivorous gamefish species (Minns 1981; Matuszek et al. 1988, 1990). Based on the results of Matuszek et al. (1988) the proportion of the fish species richness comprised by small fish species would be predicted to be over 50% in lakes <10 ha. In this general area of Ontario, most exclusively nongamefish assemblages would also be expected in lakes <10 ha in size (Minns 1981). In the Algoma lakes, a lake depth of ~5 m would be expected for a lake size of 10 ha. Larger fish species, such as percids and centrarchids, may utilize zooplankton primarily during their earlier life stages (Seaburg and Moyle 1964; Persson 1983), leading to widely fluctuating influences on zooplankton abundance related to fluctuating year-class strength (Mills et al. 1987; Mills and Forney 1988). In contrast, gape-limited small fish species, such as the fathead minnow, may actively forage on zooplankton throughout their life histories (Held and Peterka 1974). In addition, in brook trout lakes the presence of competitors like creek chub may lead to increased zooplanktivory by brook trout (Magnan and FitzGerald 1982; Magnan 1988) a common gamefish species in lakes of the Algoma area.

An increase in species richness occurred among three of the shallowest lakes (Fig. 2), which were also strongly dominated by relatively large species (*H. gibberum*, *D. pulex*, or *S. oregonensis*). This observation is not consistent with our inference of generally greater zooplanktivory by fish in shallow lakes. However, it may be that these lakes do not actually contain fish, although based on the absence of *C. americanus* they were not classified as fishless. Lakes of such shallow depth (<2 m) have a high probability of winterkill, and while the presence of *C. americanus* is indicative of fish absence, the absence of *C. americanus* is not proof that fish are present, because other factors may control the occurrence and abundance of *Chaoborus* (Nilssen 1974; Neill and Peacock 1980; Yan et al. 1985). The simple fact that some small, very shallow, probably fishless lakes without *C. americanus* have quite species-rich zooplankton assemblages argues against negative zooplankton species interactions as an important factor affecting species richness and in turn implicates predation as a probable control. Increased fish predation pressure in small, shallow lakes may result from both the shift to a community dominated by small fish (Minns 1981; Matuszek et al. 1988, 1990) and the fact that deepwater refuges, which may be important for predator avoidance through vertical zooplankton migrations (Lampert 1987; O'Brien 1987; Ohman 1990), are limited or absent. The decline in *Daphnia* and a pattern of decreasing zooplankton mean size (Keller 1993) with decreasing depth in our lakes with fish are consistent with the expected results of heavy fish predation.

It was expected that the typically littoral species might occur only in the plankton of shallower lakes, because in these shallow lakes even the open waters may provide an essentially littoral habitat. Additionally, because lake depth was correlated with lake area, the proximity of the open lake waters to the lake shoreline in shallower (and generally

smaller) lakes may facilitate invasion by littoral species. However, while they were never particularly common, the highest occurrences of the littoral species *O. modestus* and *S. crystallina* (33 and 22% of the lakes, respectively) were observed not among shallow lakes but among fishless lakes (Table 5). This indicates that the presence of these relatively large species in the limnetic plankton may be affected by fish predation.

Predation also appears to be an important factor structuring zooplankton assemblages in fishless lakes. Even though the Algoma lakes considered here all had pH >6.0, an acidity-related component (PC3) characterized by positive correlations with *C. americanus* abundance and negative correlations with lake area, pH, Ca, conductivity, and watershed area did emerge from the PCA (Table 4). Correspondingly, lakes inferred to be fishless based on the occurrence of *C. americanus* were slightly more acidic (Table 7) than the other study lakes. However, because declines in acid-sensitive zooplankton species appear to occur quite abruptly at or below pH 6.0 (Keller et al. 1990; Havens et al. 1993), significant direct chemical effects on zooplankton in these Algoma study lakes are unlikely under current chemical conditions. Rather, the absence of fish, leading to an invertebrate-based predation system appears to be the major influence. The absence of fish from these lakes may be a natural condition; however, since recent decreases in the acidity of lakes in this area of Ontario, owing to reduced acid deposition, have been documented (Kelso et al. 1992), current chemistry may not completely reflect historical conditions. Previous chemical conditions may have influenced the fishless status of some lakes.

The occurrence or abundance of a number of zooplankton species was dramatically different in fishless lakes. *Daphnia g. mendotae*, a species very vulnerable to *Chaoborus* predation (Vanni 1988) was absent from fishless lakes (Table 5) while *A. leptopus*, a species with apparently low vulnerability to *Chaoborus* predation (Blais and Maly 1993), was most common (Table 5) and abundant (Table 6) in fishless lakes. The absence of *D. birgei* from fishless lakes (Table 5) agrees with experimental results reporting strong selection for *D. leuchtenbergianium* (now considered *D. birgei*; Kořínek 1981) by *Chaoborus* (Winner and Greber 1980) and results showing substantial reductions in *D. birgei* abundance by *Chaoborus* predation (Vanni 1988). It is also noteworthy that the occurrence of *D. pulex*, a species apparently very vulnerable to fish predation (Gailbraith 1967; Mills and Forney 1988; Dini and Carpenter 1991) but not *Chaoborus* predation (Lynch 1979) was also highest in fishless lakes (Table 5).

While cause–effect relationships cannot be proven solely with survey data, investigations at various scales are required to provide complete insights into community processes, as discussed by Frost et al. (1988). Survey data, as provided herein, form the essential link coupling theory and experimental results to the realities of the natural environment. Our empirical survey results, and the interpretations presented, are consistent with a large body of experimental findings that identify the potential importance of biological interactions, particularly predation, in structuring aquatic communities (e.g., McQueen et al. 1986; Kerfoot and Sih 1987; Carpenter 1988). This study provides lake-scale evidence for the importance of such mechanisms in regulating zooplankton community structure on a regional basis. The results further suggest that small, shallow lakes may be fundamentally different from larger, deeper lakes, with fish and invertebrate predation playing much more dominant roles in shaping zooplankton community structure.

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Zooplankton Assemblage Responses to Disturbance Gradients

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Stemberger, R.S., and J.M. Lazorchak. 1994. Zooplankton assemblage responses to disturbance gradients. Can. J. Fish. Aquat. Sci. 51: 2435–2447.

Zooplankton assemblages of 19 New England lakes were evaluated in relation to lake trophic state, riparian land use, fish assemblage features, and physicochemical factors for potential food web indicators of lake ecosystem condition or health. Principal component analysis (PCA) of species abundance data contrasted productive warmwater lakes dominated by rotifers, small cladocerans, and cyclopoid copepods and nauplii with cold-water salmonid systems dominated by calanoid copepods and large cladocerans, and with few rotifers. The use of 12 aggregate zooplankton assemblage variables based on taxonomic group, body size, life-history stage, and feeding guilds improved the amount of the explained cumulative variance (63.2%) over species data (40.3%) in the first two axes of the ordination. In a second PCA the environmental variables were constrained with respect to the zooplankton variables. This analysis identified total phosphorus, chlorophyll *a*, cold-water fish assemblages, number of introduced fish species, piscivore numbers, and the percentage of disturbed shoreline as dominant gradients. Small-bodied assemblages represented by small cladocerans, rotifers, ostracods, nauplii, and cyclopoid copepodites were associated with the most disturbed systems. The pattern of distribution among large- and small-bodied taxa from the PCA was used to formulate metrics which were then correlated to the gradients.

Des assemblages de zooplancton de 19 lacs de la Nouvelle-Angleterre ont été évalués par rapport à l'état trophique du lac, à l'utilisation des terres riveraines, aux caractéristiques des assemblages de poissons et aux facteurs physico-chimiques afin de trouver dans le réseau trophique des indicateurs potentiels de l'état de l'écosystème lacustre. L'analyse en composantes principales des données sur l'abondance des espèces a comparé les lacs tempérés productifs dominés par les rotifères, les petits cladocères, les copépodes cyclopidés et les nauplius avec les systèmes de salmonidés des eaux froides dominés par les copépodes calanoïdes et les gros cladocères et renfermant quelques rotifères. L'utilisation de 12 variables agrégées portant sur les assemblages de zooplancton et fondées sur le groupe taxinomique, la taille, le stade de développement et la guilde de nutrition a amélioré la quantité de la variance cumulative expliquée (63,2%) par rapport aux données sur les espèces (40,3%) dans les deux premiers axes de l'ordination. Dans une deuxième analyse en composantes principales, les variables environnementales étaient limitées par rapport aux variables du zooplancton. Dans cette analyse, on a identifié comme gradients dominants le phosphore total, la chlorophylle *a*, les assemblages de poissons d'eau froide, le nombre d'espèces de poissons introduits, le nombre de piscivores et le pourcentage de perturbation du littoral. Les assemblages de petits organismes représentés par les petits cladocères, les rotifères, les ostracodes, les nauplius et les copépodites cyclopidés étaient liés aux systèmes les plus perturbés. Le profil de distribution des taxons de petite et de grande tailles tiré de l'analyse en composantes principales a été utilisé pour formuler des mesures qui ont ensuite été corrélées aux gradients.

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Zooplankton possess many attributes that should make them effective indicators of lake ecosystem condition or health. They are speciose, being represented by several phyla but mostly dominated in freshwater by copepods, cladocerans, and rotifers. They often display morphological or behavioral adaptations to vertebrate and invertebrate predators (Kerfoot and Sih 1987) and have general or specialized feeding modes and food preferences (Price 1988). They respond to abiotic factors such as pH, temperature, dissolved oxygen, turbidity, salinity, heavy metals, and pesticides and display a wide range of life-history patterns, life cycles, and modes and rates of reproduction. Thus, we should expect responses from species or higher taxonomic units to factors that disrupt or alter coevolutionary relationships among species. The intermediate trophic position of the zooplankton in the food web of lakes also makes the group responsive to bottom-up as well as to top-down ecosystem processes (Carpenter et al. 1985; Vanni and Findlay 1990; Hunter and Price 1992).

Despite the importance of zooplankton as consumers of primary production and as agents of energy transfer and nutrient cycling they have not been widely used as indicators of environmental condition. Attributes of zooplankton assemblages such as body size, abundance, and taxonomic structure are understood in general ways with respect to fish predation, trophic state, and physiological preferences for temperature, pH, or salinity. However, there are few assemblage responses that are specific to a single environmental

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factor or condition and for which there is also supporting experimental evidence. The best known assemblage responses are shifts in body size with increased zooplanktivory; food web simplification with acid, copper, aluminum, or pesticide stress; and biomass increases with nutrient enrichment (Gannon and Stemberger 1978; Carpenter et al. 1985; MacIsaac et al. 1987; Siegfried et al. 1987, 1989; Havens 1991, 1993, 1994; Beaver and Crisman 1990; Tessier and Horwitz 1990, 1991; Locke 1992; Moore and Folt 1993; Havens and Hanazato 1993).

We describe zooplankton assemblage responses from 19 New England lakes as part of a 1991 Northeast Pilot Survey of the Environmental Monitoring and Assessment Program – Surface Waters (EMAP–SW), which is one ecological component of the Environmental Monitoring and Assessment Program (EMAP). This monitoring program uses a probability-based sample-selection design to provide quantitative assessments of the condition of ecological resources of estuaries and Great Lakes, surface waters (lakes, reservoirs, rivers, and streams), wetlands, forests, arid lands, and agroecosystems within the United States. These assessments will attempt to identify the extent, magnitude, and location of degradation or improvement in the environment (Larsen et al. 1991; Paulsen et al. 1991). Zooplankton is one of several biological indicators being evaluated to meet EMAP–SW objectives.

Our objectives was to identify the major zooplankton assemblage responses from 19 study lakes in the northeastern United States and to identify the probable environmental gradients underlying these responses. Lakes chosen over broad geographical areas are likely to have multiple gradients and complex system responses. Therefore, analytical approaches become increasingly important in the identification of environmental gradients and in the interpretation of the responses. This study demonstrates an approach to this problem. We first used simple principal components analysis (PCA) of species abundance data to identify major patterns and associations of species in the data set. We then used the species distribution pattern of the first two PCA axes to suggest ways to aggregate data based on feeding guilds, taxonomic group, and body size, and for formulating richness and abundance metrics. The trophic-structure metrics were then used in a canonical form of PCA that identified the dominant environmental gradients. The richness and abundance metrics were then correlated with these gradients. Although there is a growing need for biological indicators of environmental condition, this use of the zooplankton is still in a formative stage and interpretation of assemblage responses should be accompanied by well-designed experiments.

Methods

Twenty New England lakes, to one of which access was denied, were selected from five states along a latitudinal gradient from Rhode Island to northern Maine. The lakes reflect the prevalent types and extent of human disturbances in the region (agriculture, residential development, fish stocking, and silvicultural impacts) and the range of size and dominant fish assemblages (Larsen and Christie 1993) (Table 1). Prior to the field survey the only information available on fish stocks was from state sources. For the sake of classification the lakes were grouped according to size (small vs. large) and ability to support salmonid or warmwater fish assemblages (cold vs. warm). Cold-water lakes ranged in size from 0.07–5.64 km^2, had total phosphorus concentrations from 0.9–11 μg/L, and in most instances supported reproduction of salmonid fish species (Table 1). Warmwater lakes ranged in size from 0.18–5.37 km^2, had total phosphorous concentrations from 4.5–30 μg/L, and did not support reproduction of salmonids even if they were present because of stocking practices. One lake (Black Pond), originally thought to represent a small warmwater system, supported large numbers of brook trout (*Salvelinus fontinalis*). Overall, the group of warmwater lakes was considerably more productive than the coldwater lakes.

Each lake was sampled once for zooplankton with a single vertical net tow taken from the deepest portion of the lake from 0.5 m off the bottom to the surface during an 8-wk sampling period (July and August 1991). We decided to take just a single vertical tow because a recent study of 146 northeastern lakes indicated that sample variance among three replicate tows at the same location and time was very small (<9%) relative to among lake variance (80–95%) for zooplankton abundance data (Tessier and Horwitz 1991). Spatial error associated with different locations in the lake was not assessed. This component of variance has been shown to be a function of sampling scale, depth, body size, and mean density (Pinel-Alloul et al. 1988). Two nets were fitted to a single harness. A cone net (30 cm diameter, 202 μm mesh) was used for macrozooplankton (4:1 net length to diameter ratio) and a Wisconsin net (48 μm mesh) with a 15-cm-diameter and 25-cm-long reducing collar for the microzooplankton (7:1 net length to diameter ratio) (C. Williamson, Department of Biology, Lehigh University, Bethlehem, PA, unpublished data). This design provided macrozooplankton samples free of net phytoplankton and debris, which facilitated enumeration with a stereomicroscope. The fine-mesh net provided high filtration efficiency for microzooplankton without compromising collection of small soft-bodied rotifers. The screened cod ends were submerged for 1–3 min in CO_2-charged water (1 tablet of Alka-seltzer™ in 500 mL of water) and the zooplankton transferred to buffered formalin (Twenty Mule Team Borax™ adjusted to pH 7.6–7.8 (R.C. Metcalf, Lockheed Engineering and Sciences Co., Las Vegas, NV, personal communication) and sucrose to give a final concentration of 4% (Lind 1979; Haney and Hall 1973).

Crustaceans, rotifers, and *Chaoborus* were identified to species using a variety of keys and references (Cook 1956; Brooks 1957; Edmondson 1959; Deevey and Deevey 1971; Brandlova et al. 1972; Koste 1978; Smith and Fernando 1978; Stemberger 1979, 1990; Korínek 1981; Dussart and Fernando 1990; Thorp and Covich 1991). Zooplankton caught in the coarse mesh net (excluding the rotifer *Asplanchna*) were enumerated using a grooved Plexiglas counting cell (10-mL capacity) under 100× of a stereomicroscope. Zooplankton caught only in the fine mesh net such as immature bosminids (<0.2 mm long), nauplii, rotifers, and small adult copepods like *Tropocyclops extensus* and small copepodites (<0.6 mm long) were counted using an inverted microscope. In rare instances where immature stages of crustaceans such as *Bosmina* passed through the coarse-mesh net but were retained in the fine mesh, the standardized abundances from the fine-mesh net were added to the standardized abundances of counts from the large-mesh net.

TABLE 1. Location and major limnological features of the 19 northeastern study lakes. P-T = total phosphorus; Cl = chloride ion; Chl *a* = chlorophyll *a*; Pisc = total abundance of adult piscivores caught in gillnets, trapnets, and seines for a standardized fishing effort; IFS = number of introduced fish species; NNGL = number of taxa of non-nest- guarding lithophils; %ShD = mean percent of disturbances at 10 monitoring sites in a lake; Y = trout present; I = trout introduced, nonreproducing; N = trout not present. Lake codes are as used in Fig. 2–4. For other land use and fish variables see Larsen and Christie (1993).

Lake	State	Lake code	Area (km^2)	Max. depth (m)	Secchi depth (m)	P-T (μg/L)	Cl (μeq/L)	pH	Chl *a* (μg/L)	Pisc	IFS (no.)	NNGL (no.)	% ShD	Trout
						Small, warm								
Abenaki	VT	AB	0.18	3.5	3.5	8.8	24	8.05	4.22	483	1	0	40	N
Black	ME	BL	0.23	4.3	4.3	11.0	78	8.01	3.55	34	0	2	20	Y
Ticklenaked	VT	TI	0.19	15.5	1.9	14.0	296	8.4	6.26	449	3	2	40	N
French	NH	FR	0.17	11.4	1.95	14.0	195	7.46	11.3	10	5	0	50	I
Mashapoag	RI	MA	0.28	4.0	1.3	30.0	1707	8.30	21.4	147	5	0	90	N
						Large, warm								
Kenoza	MA	KE	1.00	16.0	2.8	7.8	774	7.93	6.52	334	4	0	40	N
Torsey	ME	TO	3.12	12.5	5.25	4.5	59	7.77	3.19	73	2	1	60	N
Groton	VT	GR	1.68	10.5	2.75	5.0	35	7.48	6.52	155	3	1	60	N
Fairlee	VT	FA	1.87	14.2	7.45	7.9	139	8.07	2.08	95	4	2	80	I
Joes	VT	JO	1.60	27.3	4.1	13.0	110	8.20	4.01	380	2	1	80	Y
Webster	MA	WE	5.37	13.2	3.9	8.6	400	7.61	6.07	91	8	0	100	N
						Small, cold								
Upper	ME	UP	0.07	4.5	2.65	11.0	7	7.61	6.77	19	0	1	0	Y
Hunnewell	ME	HU	0.26	12.0	4.6	7.5	8	7.88	5.52	15	0	2	10	Y
Russel	NH	RU	0.16	23.5	13.3	0.9	16	6.79	1.96	6	2	1	20	I
Tewksbury	NH	TE	0.19	14.9	6.75	1.8	228	7.49	1.30	27	4	3	40	I
						Large, cold								
Debsconeag	ME	DE	1.30	41.0	5.8	3.0	13	7.33	3.05	49	3	7	20	Y
Harrington	ME	HA	4.53	37.0	4.1	6.8	39	7.38	4.91	42	2	9	0	Y
Nubanusit	NH	NU	2.89	23.3	7.6	7.0	19.5	6.58	2.17	158	3	4	30	Y
Nesowadnehunk	ME	NE	5.64	15.5	2.9	0.9	8	7.27	3.27	28	1	1	50	Y

Copepods (>0.6 mm long) and cladocerans (>0.2 mm long) that were caught in the fine net were ignored because they would be enumerated in the coarse-mesh net. Two- to 5-mL subsamples were placed in a counting cell with a 2-mm-wide transverse channel with the bottom covered with 35 × 60 mm glass coverslip sealed with mounting media. Three replicate subsamples were taken so that a total of 300–500 individuals were counted for each net sample. Abundance estimates were based on the depth of the water column having >0.1 mg/L of dissolved oxygen and were expressed as number per litre. Standardized abundances of species from the counts of both nets were combined into a single lake by species matrix for statistical analysis. *Chaoborus* and aquatic mites were probably not effectively sampled using the sampling technique. These taxa, however, were included in exploratory analyses of the species data but were omitted from the ordination using aggregate variables because their low PCA scores suggested they were either not important or were inadequately sampled.

Fish species composition was estimated through use of a variety of gear, including experimental gillnets, trap nets, minnow traps, eel pots, beach and minnow seines, and boat electrofishers (Pollard and Peres 1991). Fish species composition was used to build structural and functional variables indicative of assemblage type or character such as species richness; number of native taxa, number of introduced taxa; and guilds related to breeding, feeding, tolerance, and taxonomic class.

Physicochemical variables (except pH) and zooplankton species and web variables were $\log_e(x + 1)$ transformed to adjust for 0 values. PCA used the correlation matrix in the program CANOCO version 3.1 (ter Braak 1988). The pattern of species distribution revealed in the first two axes of the ordination suggested ways to aggregate taxa based on taxonomic group, body size, life-history stage, and feeding modes. A constrained PCA, also known as redundancy analysis, was done on the aggregate variables using a subset of 12 environmental variables and the forward selection procedure in CANOCO. These environmental variables included the percentage of shoreline with disturbance sites (docks, access sites, boat houses, swimming beaches, buildings, lawns, roads, etc.), number of native fish species, number of introduced fish species, number of species of non-nest-guarding lithophils (i.e., salmonids and other non-nest-guarding species that deposit eggs on rocky substrates), total N, pH, total P, Secchi disk depth, chlorophyll *a*, and zooplanktivore and piscivore fish abundances. These variables were chosen from a larger suite of morphometric, water chemistry, fish, and land-use variables for the following reasons. They were ecologically plausible as explanatory factors in zooplankton responses and were not highly correlated with other environmental variables of interest, they had high correlations with zooplankton variables in linear regression models, and/or they consistently entered the PCA model early in the forward selection procedure even though they may not have been statistically significant.

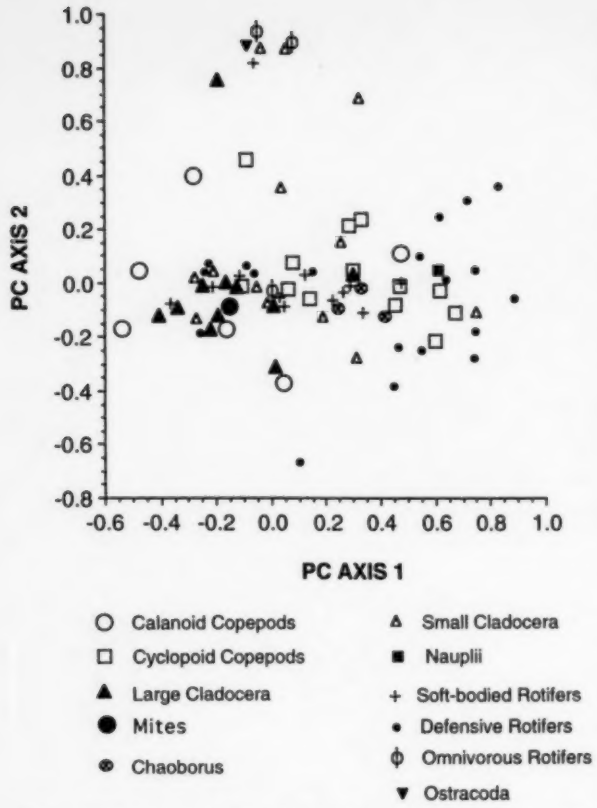

FIG. 1. PCA of zooplankton in species space. Coordinates of taxa are species scores for axes 1 and 2 given in Table 2.

A Monte Carlo test of significance (99 permutations) was done for each variable that was included in the model (ter Braak 1988). Why the number of species of non-nest-guarding lithophils should be important is not obvious. We believe that it is a surrogate for a suite of qualities associated with oligotrophy such as high water clarity, low temperatures, well-oxygenated bottom waters, and perhaps indicative of the relative inefficiency of zooplanktivory by salmonids. The larger suite of variables that were considered but not chosen because they did not meet the selection criteria given above were NH_4, NO_3, SO_4, Cl, ANC, color, K, dissolved organic carbon, conductivity, Mg, Na, SiO_2, total suspended solids, lake surface area, maximum depth, surface temperature, shoreline development factor, percent shoreline in urban development, percent shoreline in agriculture, percent shoreline in forest, percent shoreline in urban–residential development, total fish richness, total fish numbers, benthivore numbers, native pelagic fish species, native minnow species, native fish families, percent native pelagic species, percent native minnow species, percent native fish families, percent piscivores, percent omnivores, and percent invertivores.

Metrics expressing zooplankton richness and abundances were based on the pattern of species distribution from the simple PCA of abundance data. Pearson correlation coefficients were calculated between these metrics and the dominant environmental gradients identified from the constrained PCA of the abundances of the 12 aggregate variables using Systat version 5.2 (Wilkinson 1992).

Results

Species Distributions

The first two PC axes of the species abundance data explained 40.3% of the variance. PC axis 1 explained 25.3% of the variance and contrasted lakes dominated by calanoid copepods, large cladocerans, and few rotifers with lakes dominated by rotifers, small cladocerans, nauplii, and large and small cyclopoid copepods (Fig. 1; Tables 2 and 3). Armored rotifers like *Keratella crassa* and those with evasive swimming behaviors like *Polyarthra*, and small cladocerans were most abundant in systems with predatory cyclopoids such as *Mesocyclops edax*, *Orthocyclops modestus*, and *Tropocyclops extensus* (Table 2). *Skistodiaptomus pygmaeus* was the only calanoid copepod that occurred in ordination space with small-bodied assemblages, although it also was an important species in macrozooplankton-dominated systems (Fig. 1; Table 2). PC axis 2 contrasted two shallow eutrophic lakes having large-bodied and small-bodied zooplankton assemblages but differing in the nature of the dominant plant communities. Eutrophic Mashapoag Pond had high algal turbidity owing primarily to the blue-green alga *Microcystis aeruginosa* and had very high standing crops of both large (*Daphnia galeata mendotae*, >20 individuals/L) and small cladocerans (*Ceriodaphnia* and *Chydorus*, >54 individuals/L), and rotifers like *Asplanchna* and *Pompholyx*. Abenaki Pond, at the negative end of the axis, had low turbidity and numerous rooted macrophytes. *Potomogeton* was present throughout the water column in most of the lake and *Nymphaea* lined much of the shoreline. The dominant zooplankters were *Daphnia catawba* (15.7 individuals/L), *Holopedium* (5.1 individuals/L), and the calanoid copepod *Aglaodiaptomus spatulocrenatus* (1.4 individuals/L). The large colony-forming rotifer *Conochilus unicornis* (176 individuals/L) had the highest negative loading of the microzooplankton with this axis (Fig. 2; Table 2).

Aggregate Variables

The former PCA on species abundances revealed that taxonomic class, body size, and feeding mode (e.g., dominance of selective grazers like calanoid copepods vs. cyclopoid omnivores of PC axis 1) characterized the main differences in species organization among the lakes. This pattern led to the formulation of 12 new variables modeled as components of a zooplankton web (excluding *Chaoborus* and water mites) where species were aggregated based on taxonomic association, body size, life-history stage (size), and herbivorous or omnivorous feeding habits (Tables 2 and 3; Fig. 1). A PCA of these new variables substantially improved the explained variance of the first two axes of the ordination relative to species abundance data (63.2 vs. 40.3%, respectively).

The dominant environmental gradients associated with the zooplankton assemblages were identified using redundancy analysis. This canonical ordination form of PCA detects the patterns of variation in the zooplankton variables that are best explained by the observed environmental variables. The resulting ordination diagram expresses both the patterns of variation of the zooplankton assemblage variables and of the lakes and their relationship with each of the environmental variables (Fig. 3 and 4). Redundancy analysis

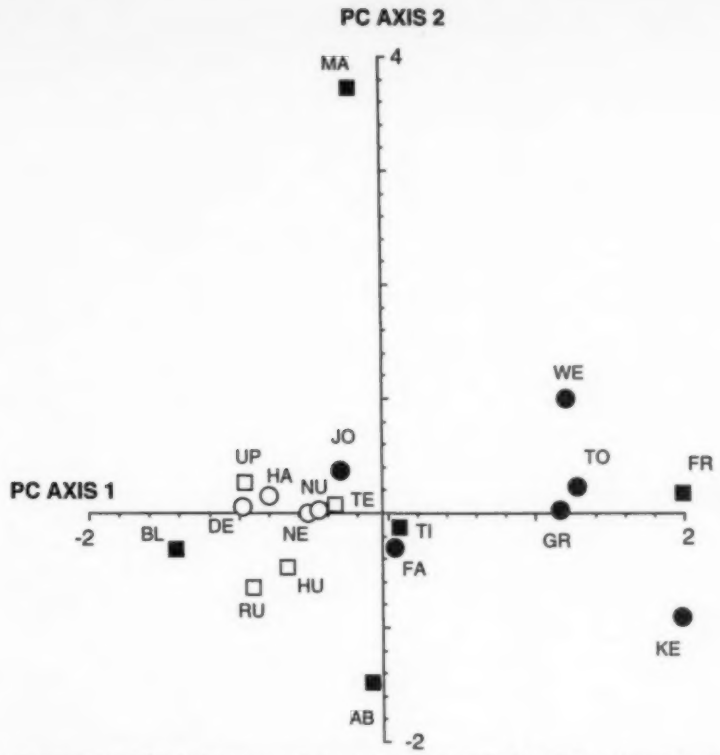

FIG. 2. Zooplankton PCA in lake space. Lake codes are identified in Table 1. Symbols designate lake categories. Open circles = large cold; open squares = small cold; closed circles = large warm; closed squares = small warm. Negative scores of PC axis 1 are associated with salmonid fish and large-bodied zooplankton assemblages and positive scores with warmwater fish and small-bodied zooplankton assemblages. PC axis 2 contrasts two warmwater lakes with visual predation refugia for large-bodied species of zooplankton. MA has high algal turbidity and AB has abundant submerged macrophytes (see text for explanation).

applied to the aggregate variables accounted for 37.9% of the explained variance (eigenvalue = 0.38) in axis 1 and 14.6% of the variance in axis 2, (eigenvalue = 0.15) (Fig. 3). Monte Carlo permutation tests (99 unrestricted permutations) on canonical axis 1 was highly significant ($p = 0.01$). Similarly, axis 2 was significant ($p = 0.01$) using the eigenvector of axis 1 as a covariable (ter Braak 1988). Six environmental variables made significant individual contributions ($p < 0.03$, 99 permutations) to explain the gradients in the zooplankton web variables using the forward selection procedure. These six variables explained 55.2% of the total variance in axis 1 and 21.4% of the variance of axis 2 for a total contribution of 76.6% for both axes. The web variable – environment correlations with the first two axes was 0.94 and 0.87, respectively, suggesting that the environmental variables account for the main variation in the zooplankton assemblage responses. Total P concentration had the highest contribution to explained variance (27%, $p = 0.01$), followed by chlorophyll *a* (10%, $p = 0.02$), non-nest-guarding lithophils (10%, $p = 0.02$), the number of introduced fish species (7%, $p = 0.02$), the percentage of shoreline with human disturbances (7%, $p = 0.02$), and piscivore abundance (6%, $p = 0.03$). Axis 1 defined a gradient contrasting low total P concentration of coldwater lakes with high total P concentration of warmwater lakes. Variables indicating disturbance such as the number of introduced fish species, percentage of disturbed shoreline, and high chlorophyll *a* concentrations dominated warmwater lakes (Fig. 3 and 4). Only Upper Pond, a relatively pristine cold-water lake, occurred in ordination space with the warmwater lakes. This lake had naturally high concentrations of total P (11 μg/L) and relatively high standing stocks of zooplankton including a predominance of small-bodied forms (Table 3; Fig. 3 and 4).

Because chlorophyll *a* entered the forward selection procedure of CANOCO after total P there is some independence in these variables. This was influenced primarily by Mashapoag Pond, which had the highest chlorophyll *a* concentration and had the most disturbed watershed in the data set (Table 1; Fig. 2 and 4). If this lake is omitted from the constrained ordination, chlorophyll *a* does not enter the model. All other variables, however, enter as before following total P concentration; the trophic gradient and the significance of the first axis is unchanged. The unexplained variance in the ordination models is likely attributable to a variety of factors including stochastic events such as storms, episodic runoff, mixing events, and the seasonal succession of species over the 8-wk sampling period. Differences among field crews and unmeasured environmental variables such as pesticide residues, phytoplankton composition, and interactions among environmental variables might also contribute to unexplained variance.

TABLE 2. PCA species scores for 19 northeastern Lakes. PC axis 1 coefficients are arranged in ascending order and correspond to the coordinates of points in Fig. 1. Macro- and micro-zooplankton categories refer to the catch in the coarse- and fine-mesh nets, respectively. Code refers to the web variable to which species was assigned in Table 3 and Fig. 3. 1 = CycO; 2 = CalO; 3 = CalH; 4 = CalcH; 5 = CyccH; 6 = CladO; 7 = LCladH; 8 = SCladH; 9 = Naup; 10 = RotH; 11 = RotO; 12 = OstrH; 13 = Chao; 14 = Mites. For explanation of code names see Table 3.

	PC axis 1	PC axis 2	Code
Eigenvalues	0.251	0.215	
Cumulative explained variance (%)	25.3	40.3	
Macrozooplankton			
Calanoid copepodids (>0.6 mm)	−0.54	−0.17	4
Leptodiaptomus minutus	−0.48	0.04	3
Leptodora kindtii	−0.40	−0.13	6
Daphnia schodleri	−0.34	−0.09	7
Eubosmina longispina	−0.27	0.01	8
Diaphanosoma brachyurum	−0.27	−0.13	7
Daphnia longiremis	−0.25	−0.02	7
Daphnia sp1	−0.22	−0.18	7
Polyphemus pediculus	−0.20	0.05	8
D. galeata mendotae	−0.19	0.75	7
Daphnia pulicaria	−0.19	−0.12	7
Acari (water mites)	−0.18	−0.05	14
Epischura lacustris	−0.18	−0.17	2
Daphnia pulex	−0.16	0.00	7
Daphnia sp2	−0.12	−0.02	7
Cyclops venustoides bispinosus	−0.11	−0.01	1
Diacyclops thomasi	−0.09	0.45	1
Chydorus brevalibris	−0.05	0.86	8
Sida crystallina	−0.05	−0.02	7
Ostracoda	−0.05	0.86	12
Eubosmina tubicen	−0.01	−0.07	8
Daphnia retrocurva	0.01	−0.09	7
Holopedium gibberum	0.02	−0.31	7
Eucyclops neomacruoides	0.03	−0.04	1
Alona spp.	0.04	0.35	8
Aglaodiaptomus spatulocrenatus	0.05	−0.37	2
Ceriodaphnia lacustris	0.05	0.87	8
Acanthocyclops robustus	0.08	0.07	1
Cyclops scutifer	0.14	−0.06	1
Chydorus sp.	0.19	−0.13	8
Chaoborus flavicans	0.23	−0.08	13
Diaphanosoma birgei	0.26	0.15	7
Ergasilis chatauquaensis	0.29	0.21	1
Chaoborus spp.	0.29	−0.01	13
Daphnia dubia	0.30	0.03	7
Macrocyclops albidus	0.30	0.03	1
Daphnia catawba	0.31	−0.28	7
Bosmina longirostris	0.32	0.68	8
Chaoborus punctipennis	0.41	−0.12	13
Mesocyclops edax	0.46	−0.08	1
Orthocyclops modestus	0.47	−0.02	1
Skistodiaptomus pygmaeus	0.49	0.11	3
Cyclopoid copepodites (>0.6 mm)	0.60	−0.21	5
Daphnia ambigua	0.75	−0.11	8
Microzooplankton			
Collotheca sp.	−0.35	−0.09	10
Synchaeta kitina	−0.29	−0.10	10
Calanoid copepodites (<0.6 mm)	−0.28	0.40	4
Keratella taurocephala	−0.24	−0.18	10
Keratella armadura	−0.24	0.04	10
Conochilus hippocrepis	−0.24	0.04	10

TABLE 2. (*Concluded*)

	PC axis 1	PC axis 2	Code
Monostyla closterocerca	−0.23	0.04	10
Monostyla stenroosi	−0.23	0.04	10
Colurella uncinata	−0.23	−0.01	10
Notommata copeus	−0.22	−0.18	10
Keratella hiemalis	−0.17	−0.01	10
Lepadella cf. *rezvoyi*	−0.16	−0.14	10
Testudinella patina f. trilobata	−0.16	−0.14	10
Bdelloid rotifers	−0.16	−0.14	10
Kellicottia longispina	−0.15	−0.09	10
Anuraeopsis fissa	−0.14	−0.14	10
Cephalodella cf. globata	−0.12	−0.02	10
Lecane cf. pelatis	−0.11	−0.01	10
Pompholyx sulcata	−0.11	0.78	10
Filinia terminalis	−0.09	0.06	10
Trichocerca cylindrica	−0.08	−0.07	10
Synchaeta asymmetrica	−0.07	0.07	10
Keratella hispida	−0.06	0.03	10
Asplanchna brightwelli	−0.06	0.86	11
Keratella robusta	0.00	−0.03	10
Epiphanes pelagica	0.01	−0.09	10
Collotheca pelagica	0.01	−0.09	10
Asplanchna herricki	0.02	−0.05	11
Gastropus hyptopus (large form)	0.02	−0.05	10
Keratella quadrata	0.02	−0.05	10
Lepadella patella	0.02	−0.05	10
Synchaeta pectinata	0.06	−0.14	10
Asplanchna priodonta	0.07	0.90	11
Trichocerca rousseleti	0.09	0.00	10
Concochilus unicornis	0.10	−0.67	10
Collotheca mutabilis	0.13	0.03	10
Keratella earlinae	0.15	0.04	10
Collotheca libera	0.23	−0.06	10
Tropocyclops prasinus	0.27	0.21	1
Collotheca balatonica	0.28	−0.03	10
Ploesoma truncatum	0.29	0.21	10
Ploesoma lenticulare	0.29	−0.02	10
Ascomorpha saltans	0.30	0.01	10
Conochiloides sp.	0.30	0.03	10
Keratella sp.	0.30	0.03	10
Trichocerca capucina	0.30	0.03	10
Trichocerca porcellus	0.30	0.03	10
Gastropus stylifer	0.33	−0.11	10
Synchaeta stylata	0.37	0.16	10
Ascomorpha ecuadis	0.45	−0.38	10
Hexarthra mira	0.47	−0.24	10
Trichocerca pusilla	0.47	−0.24	10
Trichocerca stylata	0.47	−0.24	10
Gastropus hyptopus	0.48	0.00	10
Kellicottia bostoniensis	0.54	0.10	10
Filinia longiseta	0.55	−0.25	10
Trichocerca similis	0.56	0.27	10
Polyarthra remata	0.59	0.26	10
Nauplii	0.62	0.00	9
Cyclopoid copepodites (<0.6 mm)	0.63	−0.02	5
Polyarthra major	0.63	0.01	10
Trichocerca multicrinis	0.65	0.00	10
Tropocyclops extensus	0.67	−0.12	1
Polyarthra euryptera	0.72	0.30	10
Polyarthra vulgaris	0.74	−0.28	10
Conochiloides dossuarius	0.75	−0.18	10
Chromogaster ovalis	0.75	0.04	10
Keratella cochlearis f. typica	0.83	0.36	10
Keratella crassa	0.89	−0.06	10

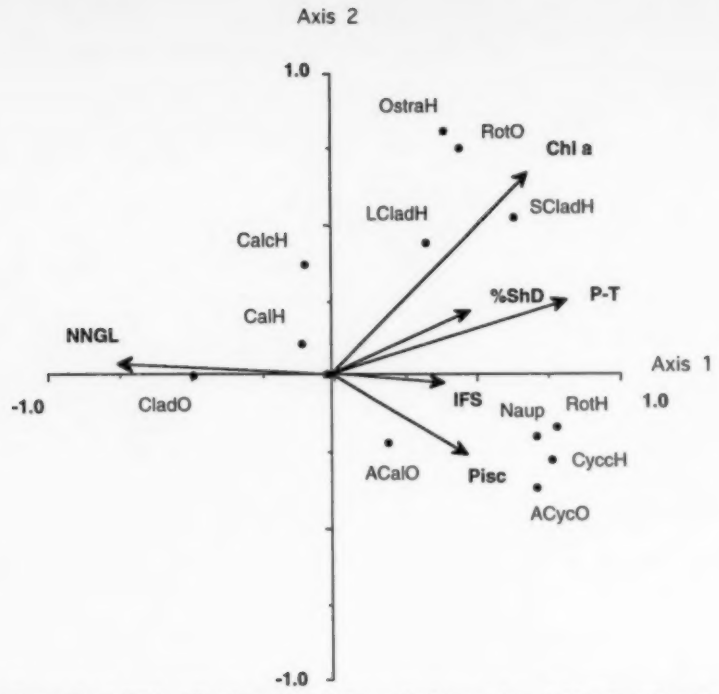

FIG. 3. Constrained PCA ordination plot of 12 zooplankton web variables for 19 northeastern lakes showing relationships of 6 significant environmental variables determined from the forward-selection procedure. Positions of aggregate variables correspond to their PCA scores from the constrained ordination. Each arrow represents the direction of increasing magnitude of an environmental gradient relative to the first two PCA axes. The length of the arrow represents the amount of variance in the environmental variable and the arrow point represents high-magnitude values. Values at the origin represent the mean value for the variable taken over the entire data set. NNGL = non-nest-guarding lithophils; IFS = no. of introduced fish species; P-T = total phosphorus; Chl *a* = chlorophyll *a*; %ShD = mean percentage of disturbances at 10 monitoring sites in a lake; Pisc = total abundance of adult piscivores for standardized fishing effort. Aggregate web variables defined in Table 3.

The distribution of aggregate variables was consistent with the PCA of species variables. Microzooplankton such as rotifers, small cyclopoid copepodites, nauplii, and large cyclopoids (such as *Mesocyclops edax*) dominated lakes with higher levels of disturbance (Table 2; Fig. 3). In contrast large calanoid herbivores and omnivores (such as *Epischura lacustris* and *Leptodora*) tended to be more prevalent in less disturbed cold-water lakes.

Zooplankton Metrics

The distribution of species along PC axis 1 suggested two prominent patterns that might be used to formulate metrics to characterize ecological condition. First, most large-bodied taxa except *Chaoborus* tended to have negative PCA scores while many small-bodied species had positive scores (Fig. 1; Table 2). Second, abundances of most species increased with increasing trophic state (Table 3). Therefore, richness related to taxonomic unit and body size might be used to characterize the level of disturbance. For example, high richness values of large-bodied taxa such as *Daphnia* and calanoid copepods were correlated with low disturbance levels whereas high richness and abundances of small-bodied taxa such as *Ceriodaphnia* or rotifers were correlated with high levels of disturbance (Fig. 3; Tables 3 and 4).

Discussion

Zooplankton as Indicators of Lake Typology and Disturbance

The results of this study indicate that nutrients, chlorophyll *a*, land use, and fish variables are important predictors of the structure of zooplankton assemblages. Lake trophic state (as distinguished by total P concentration, chlorophyll *a*, and the presence of cold-water or warmwater fish stocks) accounted for the major differences in body size, taxonomic groups, and feeding guilds of the zooplankton assemblage variables. Although physicochemical factors have been historically used as corollary variables to explain zooplankton assemblage structure, information on fish assemblages and riparian land use has seldom been available for environmental analyses (Sprules 1977; Tessier and Horwitz 1991; Pinel-Alloul et al. 1989). Prominent differences in the composition and size structure of zooplankton assemblages associated with cold-water or warmwater lakes also suggest fundamental differences in the intensity or efficiency of zooplanktivory. Given that lakes were characterized with a single vertical net tow from the pelagic zone, zooplankton appear to be useful indicators of lake typology and of fish and land-use factors related to disturbance. However, statistical

TABLE 3. Abundance (no./L) of 14 aggregate zooplankton variables used in the constrained PCA. CycO = cyclopoid omnivores; CalO = calanoid omnivores; CalH = large calanoid herbivores; CalcH = calanoid copepodites; CyccH = cyclopoid copepodites; CladO = *Leptodora*; LCladH = large cladocerans; SCladH = small cladocerans; Naup = nauplii; RotO = rotifer omnivores; RotH = rotifer herbivores; OstrH = ostracods; Chao = *Chaoborus*; and Mites = water mites.

Lake code	CycO	CalO	CalH	CalcH	CyccH	CladO	LCladH	SCladH	Naup	RotH	RotO	OstrH	Chao	Mites
							Small, warm							
AB	7.69	1.42	0.00	3.17	22.10	0.00	21.49	0.21	33.41	194.56	0.00	0.00	0.00	0.01
BL	1.74	0.01	3.23	11.60	0.25	0.01	8.93	0.00	8.94	109.96	0.00	0.00	0.00	0.01
TI	1.34	0.37	0.00	0.14	8.06	0.00	11.26	1.67	54.61	154.50	0.00	0.00	0.03	0.00
FR	13.56	0.14	4.50	1.58	16.98	0.00	4.58	3.03	109.54	123.70	0.00	0.00	0.03	0.00
MA	1.58	0.00	1.26	6.39	5.03	0.00	20.64	65.14	22.01	95.36	20.96	1.15	0.00	0.00
							Large, warm							
KE	15.27	0.00	1.06	0.49	23.20	0.00	0.06	1.31	74.70	208.43	0.00	0.00	0.09	0.00
TO	1.62	0.00	2.78	2.42	3.58	0.00	5.45	0.48	23.01	150.15	0.00	0.00	0.12	0.00
GR	2.75	0.04	0.18	0.09	3.41	0.00	4.44	1.49	15.36	136.27	0.90	0.00	0.09	0.00
FA	2.88	0.02	1.76	2.10	0.49	0.00	6.34	0.00	40.17	65.68	0.10	0.00	0.01	0.00
JO	0.60	0.00	0.07	0.03	1.40	0.00	4.99	2.23	9.75	38.42	0.49	0.00	0.02	0.02
WE	4.43	0.01	0.07	0.07	3.96	0.00	0.01	5.08	33.67	159.58	1.32	0.02	0.00	0.01
							Small, cold							
UP	3.91	0.03	17.13	6.24	9.92	0.00	5.06	5.91	42.90	67.26	0.00	0.00	0.00	0.00
HU	0.07	0.03	1.95	1.13	0.00	0.02	1.82	0.00	14.29	59.18	0.00	0.00	0.02	0.00
RU	0.00	0.00	1.31	4.06	0.00	0.00	1.10	0.28	3.20	40.05	0.00	0.00	0.01	0.00
TE	1.53	0.05	0.08	0.02	1.28	0.00	3.33	1.55	4.45	24.98	0.07	0.00	0.00	0.02
							Large, cold							
DE	0.33	0.07	0.69	1.23	0.15	0.02	0.57	0.09	3.08	7.97	0.00	0.00	0.00	0.00
HA	1.01	0.06	3.03	3.11	0.69	0.00	1.78	0.31	13.14	9.62	0.00	0.00	0.00	0.00
NU	0.34	0.10	1.86	1.74	3.47	0.02	0.49	0.47	11.76	21.37	0.02	0.00	0.00	0.02
NE	1.17	0.30	1.70	2.74	1.70	0.00	1.58	0.61	40.71	19.73	0.00	0.00	0.09	0.00

confidence would be improved if additional replicates had been taken to address spatial and temporal variance.

The predation ecology of rotifers was also helpful in interpreting PC axis 1. Large and small cyclopoid predators were associated with rotifers (Fig. 1; Table 2). Cyclopoids are important predators on rotifers and may drive the seasonal succession from small soft-bodied forms to defensive ones (Stemberger and Evans 1984). Hence, in these rotifer-dominated systems invertebrate predation appears to be more intensive than is generally acknowledged in the trophic-cascade model (Carpenter et al. 1985), where small herbivores are grouped without addressing the functional significance of morphology. The association of cyclopoids with defensive rotifers also suggests that these predators may be more effective at avoiding predation by fish than are most large calanoid copepods. Only *Skistodiaptomus pygmaeus* (1.1. mm body length) appeared in PC space with small-bodied assemblages (Table 2; Fig. 1). However, body lengths of this copepod in cold-water lakes of Maine often exceed 1.4 mm (R.S. Stemberger, unpublished data). The pronounced body-size and taxonomic patterns associated with the first PC axis (Fig. 1 and 3) are consistent with size-selective fish predation, small-bodied assemblages indicating greater intensity of predation by fish (Brooks and Dodson 1965; McQueen et al. 1986).

Refugia and Assemblage Responses to Specific Disturbances

Large zooplankton may persist in the presence of abundant zooplanktivores when a spatial or visual refuge exists (Shapiro 1990; Wright and Shapiro 1990; Timms and Moss 1984). Such refugia help explain the presence of large-bodied zooplankton among some lakes in this study (Fig. 2). For example, the dominance of large-bodied zooplankton assemblages in cold-water lakes having salmonids may have several causes. First, the feeding efficiency of salmonids on zooplankton is significantly less than that of centrarchids. O'Brien (1987) has shown that brook trout have a reactive distance that is one quarter that of bluegill (*Lepomis macrochirus*) when feeding on *Daphnia* at low light levels. Second, the warm temperatures of the epilimnion may provide a thermal refuge, which limits the length of time that cold-water predators such as trout may forage. Finally, the dominance of large cladocerans in mid-lake samples may represent the end of a predation gradient of zooplantivorous fish extending out from the littoral zone (Gliwicz and Rykowska 1992).

Potential visual refuges of Mashapoag and Abenaki Ponds were identified by PC axis 2 (Fig. 2). Eutrophic Mashapoag Pond had the lowest Secchi depth (0.95 m) and highest turbidity (6.8 JTU) of all lakes studied. Turbidity was attributed to high density of the blue-green alga *Microcystis aeruginosa*. High turbidity would reduce predation risk by decreasing the reactive distance of planktivores (Confer et al. 1978). The release from zooplanktivory and potentially high reproductive rates stimulated by high algal resource levels may promote the high standing stocks of large *Daphnia* found in this lake. In this instance the effect of the refugium, a consequence of watershed urbanization and high nutrient

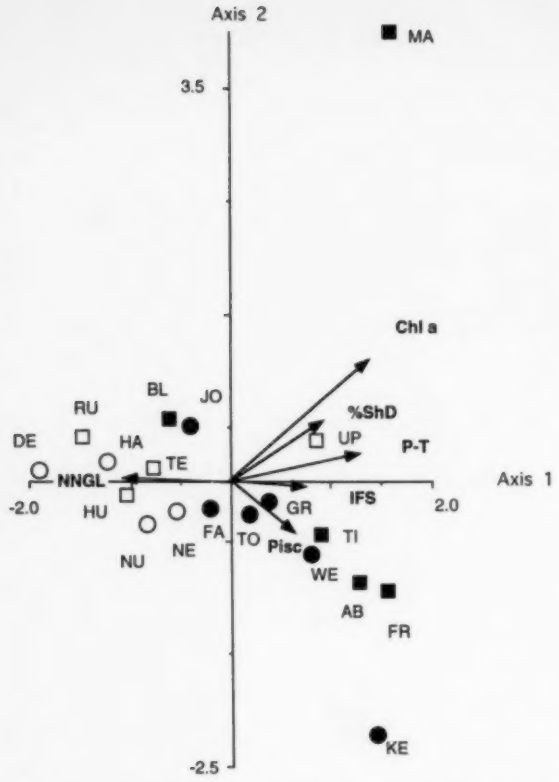

FIG. 4. Constrained PCA of zooplankton web variables in lake space showing vectors of dominant environmental factors. Vectors are approximate and do not have the same scale as zooplankton coefficients in Fig. 3. Lakes and symbols as in Fig. 2 and 3.

loading, could be viewed as an indicator of disturbance. The degraded condition of Mashapoag Pond suggests that high abundances of ostracods, small cladocerans (such as *Bosmina*, *Chydorus*, and *Ceriodaphnia*, and of a variety of rotifer taxa are potentially important indicators of disturbance (Table 4).

The assemblage of Russel Pond suggested acid stress even though its pH was circumneutral. The dominant zooplankters (*Keratella taurocephala*, *Daphnia catawba*, and *Holopedium*) are typical members of acid lakes of this region (Brett 1989). This assemblage was the only one lacking cyclopoid predators. Consequently, its food web was greatly simplified owing to the absence of zooplankton omnivores. Natural reproduction of brook trout does not occur in Russel Pond despite annual stocking by the state. Presumably, acid meltwater during the spring thaw may cause egg and fry mortality (R.M. Hughes, ManTech Environmental Technologies, Corvallis, OR, personal communication; Gubala et al. 1991).

Zooplankton Aggregate Variables

The separation of lakes in the constrained PCA of aggregate variables was similar to results based on the simple PCA of species (Fig. 2 and 4). Species data gave a more refined separation of lakes than did aggregate variables even though the former explained less of the variance. Most cold-water lakes had large-bodied low-biomass zooplankton assemblages whereas warmwater lakes had small-bodied high-biomass assemblages. Aggregate variables did not reveal the probable predation refuge of Abenaki Pond. However, both aggregate and species variables indicated the presence of salmonids in Joes Pond and Lake Fairlee even though trout were not captured as a result of gillnet restrictions. The presence of salmonids in these lakes was later confirmed by conversations with local fishermen. Ordination relationships with fish metrics are probably conservative because trout were not included in fish-assemblage variables of Joes Pond and Lake Fairlee. Black Pond was originally selected as a small warmwater lake based on limnological characteristics of the central basin. However, numerous cold-water springs along the margin of the lake permitted survival of brook trout despite polymixis and warm bottom-water temperatures (22°C). Again, the zooplankton assemblage indicated the presence of salmonids.

Zooplankton Metrics

Metrics expressing richness and abundance are intuitively appealing because of their simplicity and expected direction of response to disturbance intensities. This study also suggests that richness and abundance of size-based taxonomic metrics can identify opposite ends of environmental gradients (Table 4). Therefore, total richness or total abundance may be uninformative or even misleading when used to characterize the level of disturbance. Although richness of large cladocerans decreases with disturbance, abundance may increase (Table 4). Therefore, efforts to develop metrics of ecological condition or ecosystem health should provide explicit relationships or correlations with the pertinent environmental gradients.

Conclusions

Because of the small number of lakes in this study some important gradients, such as pH, are not well represented or have been excluded. Therefore, we view this study more as an approach or process for developing a zooplankton indicator rather than as the method itself. Nonetheless, some important conclusions can be made as to the efficacy of the approach. Firstly, aggregation of zooplankton taxa based on a food-web model is a logical extension of the results of the ordination of species-abundance data. Although aggregation of species into trophic-structure variables has time- and cost-saving advantages, there may be information and sensitivity loss owing to compensatory responses of component taxa along a gradient (Frost et al. 1992). Nevertheless, aggregate variables based on trophic structure have clear advantages in the amount of the variance they explain by reducing noise and zoogeographic effects. Overall, they appear to capture the major zooplankton web responses appropriate to the regional scale of EMAP. Aggregate variables can be easily generated without a high degree of taxonomic training and the improvement in the cumulative amount of explained variance found in this study is consistent with other findings (Sprules 1984; Siegfried et al. 1987). These web variables are also consistent with notions of a five-level trophic structure in pelagic ecosystems (phytoplankton, herbivorous zooplankton, predatory zooplankton, zooplanktivorous fish, and piscivores) and, therefore, are interesting on theoretical grounds (Hairston and Hairston 1993). Moreover, zooplankton variables based on size and

TABLE 4. Pearson correlation coefficients of zooplankton assemblage attributes (metrics) with dominant environmental gradients in the 19 study lakes. Gradients are defined in Table 1. Species comprising the metrics coincide with the body-size categories given by the code numbers in Table 2. Further explanation given in the text. $*p < 0.05$.

	Chl *a*	P-T	%SHD	IFS	Pisc	NNGL
			Richness			
Large cladocerans	−0.495*	−0.492*	−0.555*	−0.469*	−0.282	0.507*
Large cyclopoids	0.117	0.291	0.523*	0.343	0.166	0.002
All calanoids	0.150	0.081	−0.230	0.143	−0.453	0.478*
Small cladocerans	0.295	0.155	0.412	0.465*	0.322	−0.194
Daphnia	−0.354	−0.256	−0.422	−0.430	−0.257	0.551*
Small cyclopoids	0.208	0.358	0.224	0.511*	−0.03	0.185
Rotifers	−0.203	−0.175	0.457*	0.372	−0.034	−0.047
Ceriodaphnia	0.354	0.540*	0.376	0.168	0.621*	−0.480*
Asplanchna	0.440	0.188	0.672*	0.555*	0.245	−0.170
Keratella	−0.360	−0.444	0.361	0.355	−0.187	0.210
Polyarthra	0.267	0.185	0.464*	0.579*	−0.002	−0.006
Macrozooplankton	−0.337	−0.184	−0.079	−0.069	−0.104	0.503*
Microzooplankton	−0.085	−0.081	0.581*	0.530*	0.082	−0.101
Total zooplankton	−0.114	−0.097	0.489*	0.469*	−0.016	0.048
			Abundance			
Large cladocerans	0.518*	0.544*	0.247	−0.085	0.493*	−0.334
Large cyclopoids	0.155	0.421	0.227	0.346	−0.003	−0.357
Large calanoids	0.018	0.191	−0.493*	−0.511*	−0.357	−0.042
Small cladocerans	0.880*	0.512*	0.404	0.309	0.011	−0.236
Small calanoids	0.642*	0.289	0.084	−0.016	−0.079	−0.061
Small cyclopoids	0.281	0.451	0.027	0.177	0.473*	−0.444
Ostracods	0.854*	0.474*	0.391	0.282	0.015	−0.199
Rotifers	0.341	0.583*	0.361	0.279	0.531*	−0.640*
Ceriodaphnia	0.858*	0.492*	0.428	0.321	0.039	−0.214
Asplanchna	0.857*	0.481*	0.424	0.308	0.021	−0.212
Keratella	0.178	0.206	0.531*	0.523*	−0.052	−0.381
Polyarthra	0.171	0.267	0.510*	0.698*	0.101	−0.390
Macrozooplankton	0.405	0.568*	−0.097	−0.336	0.139	−0.316
Microzooplankton	0.516*	0.695*	0.363	0.350	0.474*	−0.660*
Total zooplankton	0.533*	0.720*	0.341	0.307	0.468*	−0.660*

feeding guilds rather than species taxonomy have often improved correlations with limnological variables which arguably capture the major structural responses in the zooplankton web (Sprules and Holtby 1979; Sprules 1984).

Secondly, zooplankton assemblages respond in a predictable way to the primary gradients identified in the study lakes: trophic state, fish assemblage variables, and land use. The dominant pattern of species associations are consistent with predation theory. For example, the first axis of the PCA of species abundances suggests that microcrustaceans and rotifers having defensive morphologies and evasive behaviors are prevalent in assemblages with abundant cyclopoid predators. The ecological significance between predation and functional morphology of microzooplankton has been largely ignored in most field studies. In contrast, systems that had low intensities of disturbance had zooplankton assemblages characterized by large body size dominated by calanoid copepods, large *Daphnia*, and few rotifers. Metrics based on richness and body-size categories are potentially valuable indicators of disturbance in north temperate lakes.

Thirdly, we conclude from these data that the distribution of large *Daphnia* is consistent with its dependence on predation refugia rather than as a simple response to a disturbance gradient. This was most evident for highly disturbed lakes where algal blooms or abundant macrophytes may have limited the efficiency of zooplanktivory or in cold-water lakes where the summer epilimnion may have provided a temporary thermal refuge from salmonid zooplanktivores.

The structural responses of zooplankton assemblages to the dominant gradient (cold-water – low total P vs. warmwater – high total P) included body size, taxonomic class, and biomass. This result suggests that in larger data sets, cold-water and warmwater systems might best be analyzed separately or treated so that morphometric, hydrological, and geographic effects are held constant with respect to the environmental variables of interest. Constrained gradient analysis and the forward selection procedure of CANOCO provided an objective procedure for identifying the most probable environmental gradients underlying the zooplankton assemblage patterns. The gradients identified in this analysis are consistent with the general typological, land-use, and trophic-state factors on which the lakes had been originally classified. However, the zooplankton provided a more detailed snapshot of the differences among the lakes, the intensity of zooplanktivory, and the presence of salmonids when these fish were not sampled or not known to be present in the lake. The zooplankton assemblage also indicated early stages of acidification of Russel Pond despite its summertime circumneutral pH.

Zooplankton have significant potential for addressing issues related to lake ecosystem condition or health. The

extensive theoretical, experimental, and empirical studies underpinning zooplankton ecology should facilitate the development of zooplankton assemblage data for environmental assessment applications. New and updated taxonomic keys should also be developed to facilitate implementation of any large-scale program even if trophic structure variables are used. All metrics, but especially those based on species richness ultimately depend on a solid grounding of species taxonomy.

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Physiological Response of American Plaice (*Hippoglossoides platessoides*) Exposed to Low Salinity

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American plaice (*Hippoglossoides platessoides*) maintained under natural conditions of temperature (0–10°C), salinity (26–28 $g \cdot L^{-1}$) and photoperiod (48°N) were transferred in four consecutive seasons directly to seawater tanks at different salinities (28 (control), 21, 14, and 7 $g \cdot L^{-1}$). During each season, a major response to salinity was observed at 7 $g \cdot L^{-1}$ and a minor response at 14 $g \cdot L^{-1}$. After 42 d at the lowest salinity (7 $g \cdot L^{-1}$), plasma sodium concentrations had dropped by 28% below those of the controls, muscle water content had increased by 3%, and plasma potassium had decreased by 13%. In winter and summer, fish in the lowest salinity also had elevated plasma cortisol concentrations compared with controls. No mortality occurred at 7 $g \cdot L^{-1}$ following three 96-h survival tests conducted in October, December, and February, whereas fish transferred to fresh water died within 24 h. These results suggest that American plaice is moderately tolerant to changes in salinity and that it should not be held for aquaculture purposes in estuarine conditions at a salinity below 14 $g \cdot L^{-1}$.

Des plies canadiennes (*Hippoglossoides platessoides*), maintenues en conditions naturelles de température (0–10°C), de salinité (26–28 $g \cdot L^{-1}$) et de photopériode (48°N) ont été directement transférées à chaque saison, en eau de mer à différentes salinités (28 (témoin), 21, 14 et 7 $g \cdot L^{-1}$). À chacune des saisons, une réponse majeure au transfert de salinité a été observée à 7 $g \cdot L^{-1}$ et une réponse mineure à 14 $g \cdot L^{-1}$. Après 42 jours à la plus basse salinité (7 $g \cdot L^{-1}$), les concentrations de sodium plasmatique avaient chuté de 28% en comparaison aux témoins, le contenu en eau du muscle s'était accru de 3% et le potassium plasmatique avait diminué de 13%. En hiver et en été, les poissons à la plus faible salinité (7 $g \cdot L^{-1}$) avaient des concentrations de cortisol élevées comparativement aux témoins. Aucune mortalité n'est survenue à 7 $g \cdot L^{-1}$ lors de trois tests de survie de 96 h en octobre, décembre et février alors que les poissons transférés en eau douce sont morts en moins de 24 h. Ces résultats suggèrent que la plie canadienne est modérément tolérante aux variations de salinité et que pour des fins aquicoles en milieu estuarien, elle ne devrait pas être gardée à des salinités inférieures à 14 $g \cdot L^{-1}$.

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The recent decline in many fish stocks in eastern Canada provides support for the development of marine fish aquaculture. As a native, cold-adapted species in the Gulf and the St. Lawrence estuary, American plaice (*Hippoglossoides platessoides*) is a candidate for flatfish production in the coastal estuarine area. Scott and Scott (1988) report that American plaice has been an important species for Canadian fisheries constituting half of all flatfish landings. The existence of a developed market makes American plaice an attractive aquaculture species.

Powles (1965) investigated the natural history of American plaice and MacKinnon (1972) documented its seasonal maturation and energy storage pattern. Despite these studies, our knowledge of the biology of this species remains limited; more information is necessary as a basis for developing its culture. To evaluate its potential for culture, we investigated different aspects of the biology of the American plaice in captivity. We first obtained basic physiological data for plaice kept under natural seasonal fluctuations of salinity and temperature suggesting that American plaice adapted less easily than Atlantic cod (*Gadus morhua*) to estuarine conditions during winter time (Audet et al. 1993). American plaice is mainly a marine species that can tolerate low salinities of 20–22 $g \cdot L^{-1}$ (Scott and Scott 1988). Such salinity tolerance is not expected to be restricted to local stocks, because the study of Stott et al. (1992) suggested the presence of a

single genetic population from the St. Lawrence estuary to the eastern end of the Gulf of St. Lawrence.

The aim of the present study was (1) to evaluate the tolerance of American plaice to low salinity in terms of osmo-ionic adjustments, stress related response, and survival and (2) to examine the seasonal variation of this tolerance to assess the biological feasibility of coastal estuarine culture.

Materials and Methods

Experimental Procedures

Plaice were caught by trawl in September 1989 and June 1990 in the Gulf of St. Lawrence near Matane, Québec. They were kept under natural photoperiod, salinity, and temperature for 1–7 mo before being used in experiments. Fluorescent lights controlled by automatic timers were adjusted weekly to follow the natural photoperiod. Seawater was pumped from a depth of 15 m to reservoirs and was distributed to rearing tanks at temperatures ranging from 0°C in January to 10°C in late summer. Salinity (S) averaged 28 $g \cdot L^{-1}$ (range 24–30) over the 12-mo experimental period. Fish were fed a maintenance ration once or twice weekly, alternately with smelt (*Osmerus mordax*), capelin (*Mallotus villosus*), or a moist feed (mixture of marine fish, invertebrates, and vitamins).

Survival at low salinities was assessed through three experiments lasting 96 h each. Plaice were directly transferred from seawater holding tanks (28 $g \cdot L^{-1}$ S) to 1.5 m^3 tanks at 0, 7, 14, 21, and 28 $g \cdot L^{-1}$ salinity in December 1989 and February 1990 and at 0, 7, 14, and 28 $g \cdot L^{-1}$ S in October 1990. Twenty plaice were transferred to each experimental tank except for the freshwater tank, which received only 10 fish. Mortalities were assessed every 12 h and the dead fish were removed. Flow rates ranged from 15 to 20 $L \cdot min^{-1}$. Fish were not fed during the experiments.

Osmo-ionic adjustment and stress related response were investigated by seasonal experiments in which groups of 90 fish were directly transferred from seawater holding tanks at 28 $g \cdot L^{-1}$ S to 8-m^3 experimental tanks at 7, 14, 21, and 28 $g \cdot L^{-1}$ (transferred control) S in November 1989 and January 1990, and at 7, 14, and 28 $g \cdot L^{-1}$ salinity in April and August 1990. Ten plaice were sampled from each tank at 1, 2, 3, 4, 7, 14, 21, and 28 d after transfer in the fall and winter experiments, and at 1, 4, 7, 14, 21, 28, 35, and 42 d after transfer in the spring and summer experiments. In addition to transferred controls, ten plaice were also sampled from the holding tanks (untransferred control) on day 1 and day 28 in fall and winter, on day 1 and day 42 in spring, and on days 1, 14, 28, 35, and 42 in summer. Feeding was stopped 48 h before transfer. Plaice were fed a maintenance ration once or twice weekly, depending on temperature, from the second week of the experiments. Plaice were not fed for 72 h before and during the first week of sampling and were also starved for 72 h before each subsequent sampling. Fish were exposed to natural seasonal photoperiod and temperature during the experiments. Salinity was adjusted as described in Dutil et al. (1992).

Measured variables were plasma osmolality, sodium (Na^+), chloride (Cl^-), potassium (K^+), proteins, glucose and cortisol, blood hemoglobin and hematocrit, mean cellular hemoglobin content (MCHC, calculated), and water content of skeletal muscle. Measured covariables included total length (TL), total weight (WT), gonad weight and sex, condition index (CI), and gonadosomatic index (GSI) were calculated. Measurements and calculations followed the same methods as described in Audet et al. (1993) and Dutil et al. (1992). Mean length and weight (SE) of plaice were 30.9 (4.1) cm and 254 (141) g in fall, 32.9 (6.3) cm and 347 (263) g in winter, 33.1 (5.1) cm and 351 (234) g in spring and 31.9 (3.9) cm and 277 (133) g in summer.

The summer experiment was marked by an unidentified disease that occurred only in the transferred control fish at 28 $g \cdot L^{-1}$ salinity and resulted in many mortalities. The early stages in the disease were characterized by skin lesions. Data from the 28 $g \cdot L^{-1}$ in summer were then excluded from the general analysis. Following this episode, notes previously collected during each experiment on the type and number of lesions of the sampled fish were categorized and transformed into an ordinal variable called external condition, comprising five types of increasingly deteriorating conditions. External condition was compared among treatments to ensure that the health of individuals was equal in all other treatments.

Statistical Analysis

Principal components analysis applied to the correlation matrix and followed by VARIMAX rotation (SAS Institute Inc. 1990) was used as a variable-clustering procedure. Variables responding to an experimental treatment should associate under one of the factors and their ranking within the factor should correspond to their intensity of reaction to the treatment. Furthermore, the general intensity of the reaction to treatment will be indicated by the ranking of the corresponding factor among all factors. Following Stevens (1986), the Kaiser rule was applied, i.e., only the principal components with eigenvalues >1.0 were retained for interpretation. In addition, as the number of individuals exceeded 1000, all variables with loadings above 0.08 were declared significant at $\alpha = 0.01$. However, only those variables sharing at least 15% of their variance with a principal component, i.e., with loadings greater than 0.39, were considered as major contributors to the factor.

Data were transformed to approximate multinormal distribution for all sets of 10 fish sampled. This was achieved by using the transformation that yielded the lowest skewness averaged over all sets, a normal distribution corresponding to a skewness equal to 0 (Snedecor and Cochran 1967). Log transformation ($\ln(x_i + 1)$) was thus applied to TL, WT, GSI, muscle water content, plasma cortisol, glucose, and potassium. Three variables were first inverted by subtracting x_i from the maximum value ($(x_{imax} + 1) - x_i$); of these, plasma sodium and chloride were then log transformed and plasma osmolality was square-root transformed. The other variables needed no transformation. Following transformation, the two largest mean skewness were 0.55 (plasma cortisol) and 0.86 (GSI).

The second step of the analysis consisted of examining the responses of the variables associated in the principal components with the salinity treatment with ANOVAs. The general linear model was applied (SAS Institute Inc. 1990), because it allowed ANOVAs to be weighted by regressors (covariables). Physiological parameters were treated as dependent variables; salinity, season, and day of sampling as independent variables (classification factors); and WT, CI, and GSI as continuous covariables. Analyses were conducted

TABLE 1. Varimax rotated loadings (r) for the osmotic performance experiment complete data set. Variables were plasma sodium (Na), chloride (Cl), and osmolality (OSM); muscle water content (MWC); weight (WT) and total length (TL); gonado-somatic index (GSI); plasma proteins (PRO), blood hemoglobin (HMO), hematocrit (HMA), and mean cellular hemoglobin content (MCHC); condition index (CI); plasma potassium (K), cortisol (COR), and glucose (GLU).

	F1	F2	F3	F4	F5	F6
Na	0.97[a]	−0.09	−0.06	−0.02	−0.03	0.04
Cl	0.96[a]	−0.01	−0.01	0.10	−0.03	0.01
OSM	0.90[a]	−0.19	−0.08	−0.10	0.00	−0.02
MWC	0.51[a]	−0.18	−0.11	−0.49[a]	−0.20	0.10
WT	−0.12	0.94[a]	0.12	0.05	−0.08	0.01
TL	−0.14	0.94[a]	0.11	−0.15	−0.05	0.01
GSI	−0.06	0.65[a]	−0.03	0.29	−0.09	0.15
PRO	−0.07	0.61[a]	0.23	0.46[a]	0.20	0.04
HMO	−0.10	0.16	0.93[a]	0.00	−0.23	0.01
HMA	−0.02	0.14	0.84[a]	0.15	0.25	0.14
MCHC	−0.12	0.07	0.44[a]	−0.17	−0.70[a]	−0.17
CI	0.04	0.11	0.04	0.88[a]	−0.12	−0.03
K	−0.19	−0.07	0.20	−0.18	0.72[a]	−0.11
COR	−0.07	0.03	0.24	0.06	−0.01	0.86[a]
GLU	−0.18	−0.16	0.31	0.23	−0.02	−0.48[a]
% explained variance	26.3	23.6	17.6	12.7	10.6	9.2

[a]Values with major loadings ($r \geq 0.39$) for a factor.

using the same transformations as for principal components. Probability levels were based on partial sums of squares (type III), which assess the independent contribution of each factor (Freund and Littell 1981). When significant, the ANOVAs were followed by multiple comparisons using the Tukey–Kramer method (SAS Institute Inc. 1990). If an interaction term was significant, multiple comparisons were performed within each level of a classification factor.

Results

Survival Experiments

In the December, February, and October survival experiments, all fish transferred to water with 0 $g \cdot L^{-1}$ salinity died within 24 h, while those transferred to 28, 21, 14, or 7 $g \cdot L^{-1}$ were all alive and in good condition at the end of the 96-h test.

Osmotic Response

Principal components analysis with VARIMAX rotation facilitated the treatment and the interpretation of the large amount of data generated by this part of our study. Six significant common factors accounting for 77% of the total variance (TV) were obtained (Table 1). In view of their high degree of correlation with factor one (F1) and consequently to each other, plasma sodium, chloride, and osmolality were further represented by plasma sodium only. Similarly, WT (F2) was kept to represent WT and TL, and blood hemoglobin (F3) to represent blood hemoglobin and hematocrit. The first common factor (F1: 26% of the explained variance (EV)) was characterized by the osmo-ionic response of the animals and as a whole summarized the response to the salinity treatment. In F1, plasma sodium was predominant ($r = 0.97$; Table 1), muscle water content ranked second ($r = 0.51$), and plasma potassium, glucose, MCHC, and blood hemoglobin showed slight but significant associations ($0.10 \leq r \leq 0.19$).

The most prominent feature of the physiological response to the different salinities was the marked decrease of plasma sodium concentrations at 7 $g \cdot L^{-1}$ salinity that was observed in each season (Fig. 1). A steady state followed this strong decline; days 14–28 in fall and winter and days 21–42 in spring and summer did not differ significantly from each other. During these periods, mean plasma sodium concentrations at 7 $g \cdot L^{-1}$ salinity ranged from 114.7 to 125.1 $mmol \cdot L^{-1}$ depending on season, whereas plasma sodium on day 1 in the untransferred control varied between 160.3 and 169.4 $mmol \cdot L^{-1}$. Transfers to 14, 21, and 28 $g \cdot L^{-1}$ S induced much less daily variation in plasma sodium: the maximum difference from the untransferred control on day 1 was 12.5 $mmol \cdot L^{-1}$ at 14 $g \cdot L^{-1}$ on day 35 in spring (Fig. 1). Even when data from the 14, 21, and 28 $g \cdot L^{-1}$ S transfers were combined with those of the 7 $g \cdot L^{-1}$, the ANOVA still showed similarity between days in plasma sodium after day 14 in fall–winter and day 21 in spring–summer. These latter days will be referred to as the final experimental days or final period.

The osmotic response can be summarized as absent following transfers to 28 and 21 $g \cdot L^{-1}$, minor at 14 $g \cdot L^{-1}$, and pronounced at 7 $g \cdot L^{-1}$. Final plasma sodium concentrations following transfer to 7 $g \cdot L^{-1}$ always differed significantly ($p < 0.001$) from those in all other treatments (Table 2). Compared with the concentrations in the 28 $g \cdot L^{-1}$ transferred controls, which varied from 167.6 to 169.4 $mmol \cdot L^{-1}$ in spring, the 7 $g \cdot L^{-1}$ concentrations were substantially lower (by 42.5 and 52.1 $mmol \cdot L^{-1}$ in fall and spring, respectively), the 14 $g \cdot L^{-1}$ were slightly lower (by 5.9 and 9.4 $mmol \cdot L^{-1}$ in fall and spring, respectively), and the 21 $g \cdot L^{-1}$ concentrations were not statistically different.

Muscle water content of the plaice transferred to 7 $g \cdot L^{-1}$ followed a pattern similar to but opposite that of plasma

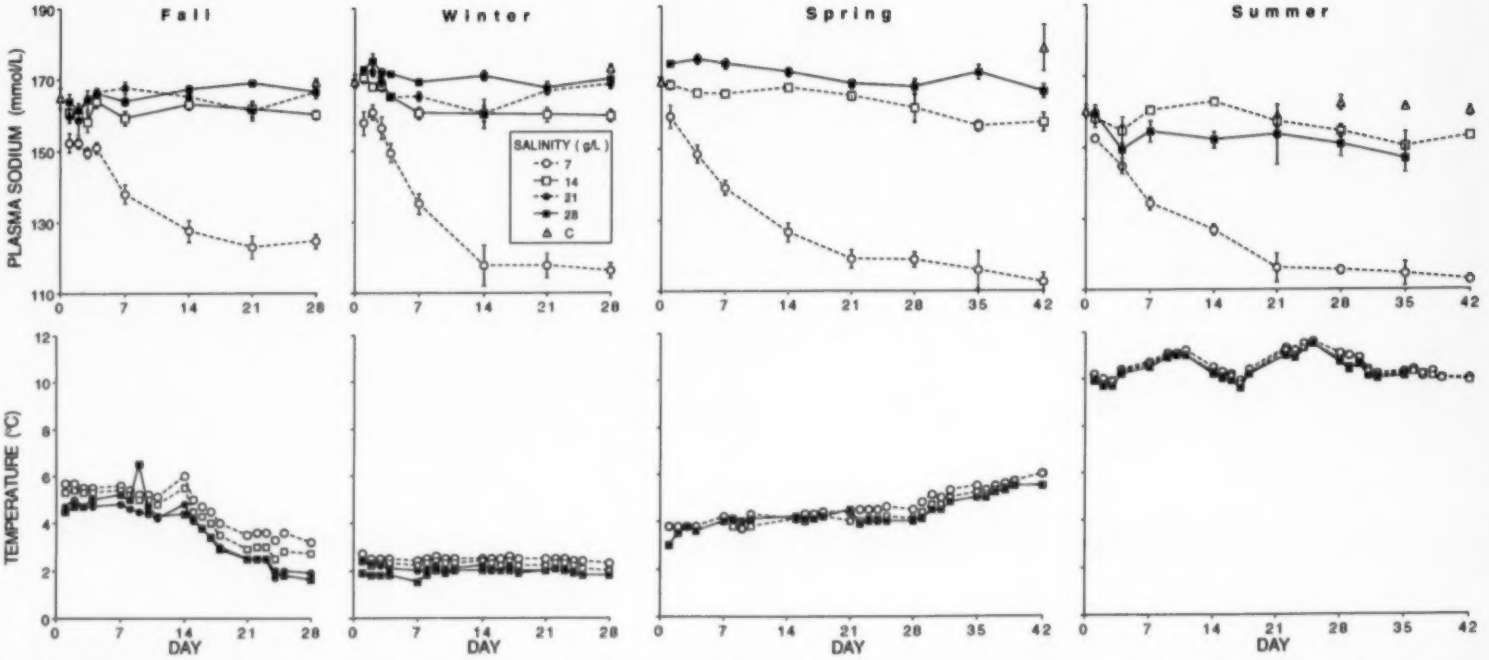

FIG. 1. Temporal changes in plasma sodium concentrations in plaice transferred directly from 28 $g \cdot L^{-1}$ to 7, 14, 21, and 28 $g \cdot L^{-1}$ salinity and in fish not transferred (C: 28 $g \cdot L^{-1}$) at each of the four seasons. Each point represents the mean value ± SE (n = 10). Daily temperatures in the experimental tanks are presented in the lower panels.

TABLE 2. Proportion of total variation (%TV) explained by salinity; seasonal averages of the transferred control (28 $g \cdot L^{-1}$) fish (Δ14); and difference between control and 7 $g \cdot L^{-1}$ transferred fish (Δ7). Summer data are excluded because of the disease contrast tests comparing 7 $g \cdot L^{-1}$ and other treatments combined are indicated by asterisks: **, $P = 0.01$; ***, $P = 0.001$.

	Plasma sodium ($mmol \cdot L^{-1}$)				Muscle water content (%)				Plasma potassium ($mmol \cdot L^{-1}$)			
	%TV	28 $g \cdot L^{-1}$	Δ14	Δ7	%TV	28 $g \cdot L^{-1}$	Δ14	Δ7	%TV	28 $g \cdot L^{-1}$	Δ14	Δ7
Fall	89	168	−6	−43***	47	81.7	0.0	2.0***	8	3.3	0.2	−0.3**
Winter	86	169	−9	−52***	47	81.8	0.5	3.3***	13	3.1	−0.3	−0.3
Spring	88	168	−8	−52***	37	81.0	0.3	2.5***	18	3.8	−0.7	−0.7

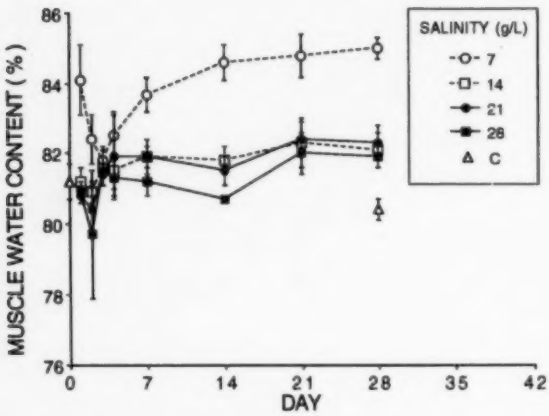

FIG. 2. Temporal variations in winter of the muscle water content in plaice transferred directly from 28 $g \cdot L^{-1}$ to 7, 14, 21, and 28 $g \cdot L^{-1}$ salinity and in fish not transferred (C: 28 $g \cdot L^{-1}$). Each point represents the mean value ± SE ($n = 10$).

sodium, i.e., after day 3 a strong increase was followed by stabilization in the final days, except on day 35, in summer; the winter response was representative of the situation in all seasons (Fig. 2). In the final period, muscle water content was always higher in the 7 $g \cdot L^{-1}$ fish compared with all other treatments, while it did not differ significantly among the 14, 21, and 28 $g \cdot L^{-1}$ transfers. Depending on season, final muscle water content in the 7 $g \cdot L^{-1}$ transferred fish increased by 2.0–3.3% compared with the 28 $g \cdot L^{-1}$ transferred controls (81.0–81.8%; Table 2). The general linear model explained 39% of the total variance of muscle water content; 47% of this variance was attributable to salinity, 23% to condition index, and less than 1% to season.

Variables with lower but significant loading values between 0.40 and 0.08 in F1 of the principal components were also analyzed and compared with plasma sodium and muscle water content. Depending on season, salinity explained 86–89% TV of the final plasma sodium concentrations and between 37 and 47% TV in muscle water content (Table 2). Only small salinity effects on the TV in plasma potassium, glucose, MCHC, and blood hemoglobin were noted, although plasma potassium showed significant variations for every season while the others did not. Plasma protein concentration was also examined as a potential indicator of variations in total plasma volume which might have influenced plasma sodium, potassium, or blood hemoglobin; general linear model analyses indicated no significant effect of salinity on plasma proteins in any of the seasons.

As reported earlier, the summer 28 $g \cdot L^{-1}$ transferred control group was diseased and, therefore, not included in the analysis of salinity effect. It was the only group to be characterized by a highly deteriorated external condition. These fish provided estimates of cortisol in plaice subjected to severe stress: high daily mean concentrations of plasma cortisol (8–36 $\mu g \cdot 100\ mL^{-1}$) were noted in this specific group (Fig. 3). Throughout the seasons, days, and salinities, most other fish had concentrations below 10 $\mu g \cdot 100\ mL^{-1}$. Exceptions were a few isolated treatments: untransferred controls on day 28 in fall, day 1 and day 28 in winter, and day 42 in spring (18–28 $\mu g \cdot 100\ mL^{-1}$), 28 $g \cdot L^{-1}$ transferred controls on day 28 in spring (22 $\mu g \cdot 100\ mL^{-1}$).

In the final period of summer, the general linear model attributed 17% of the total variation of plasma cortisol in all fish, including the diseased controls, to external condition and 14% to salinity. The mean concentrations of cortisol of the untransferred control and the 14 $g \cdot L^{-1}$ transfer group were not significantly different (2.5 and 3.6 $\mu g \cdot 100\ mL^{-1}$, respectively), the concentration of the 7 $g \cdot L^{-1}$ group was significantly higher (4.9 $\mu g \cdot 100\ mL^{-1}$) and the 28 $g \cdot L^{-1}$ diseased control group was still higher at 14.5 $\mu g \cdot 100\ mL^{-1}$. In the winter final period, the cortisol concentration in the 7 $g \cdot L^{-1}$ group was also significantly higher than in the other treatments. In the fall and spring final periods, the 28 $g \cdot L^{-1}$ transferred controls had the highest plasma cortisol concentrations (mean values of 8.0 and 12.8 $\mu g \cdot 100\ mL^{-1}$, respectively).

Seasonal Variation

Seasonal averages of final concentrations were examined only from the 14 $g \cdot L^{-1}$ *S* transfer data, because this experimental condition was the only one present in all seasons. The intensity of the seasonal variation for a variable was calculated by dividing the mean square of the seasonal effect by the mean square of the intrasample variation using all salinities. This ratio was called seasonality and ranged from 5.4 to 38.5.

The mean seasonal plasma sodium concentration varied from 156.3 $mmol \cdot L^{-1}$ (summer) to 163.9 $mmol \cdot L^{-1}$ (winter) and seasonality ratio was small (9.0). All the variation through seasons (13.5% TV) was explained by the interaction with temperature, which ranged from 2 to 12°C. Plasma potassium showed the largest seasonality (38.5), with concentration values ranging from 2.81 $g \cdot L^{-1}$ in winter to 4.00 $g \cdot L^{-1}$ in summer. All seasonal variation could be accounted for by a temperature effect (slope 0.1 $mmol \cdot L^{-1} \cdot °C^{-1}$). Plasma glucose seasonality was intermediate (20.1); seasonal concentrations declined from 47.6 $mg \cdot 100\ mL^{-1}$ in the fall to

over days 14–28 in fall and winter and days 28–42 in spring; difference between control and 14 $g \cdot L^{-1}$ transferred in fish transferred to 28 $g \cdot L^{-1}$ salinity. MCHC = mean cellular hemoglobin content. Significance levels of

Plasma glucose ($mg \cdot 100\ mL^{-1}$)				MCHC ($g \cdot 100\ mL^{-1}$)				Blood hemoglobin ($g \cdot 100\ mL^{-1}$)			
%TV	28 $g \cdot L^{-1}$	Δ14	Δ7	%TV	28 $g \cdot L^{-1}$	Δ14	Δ7	%TV	28 $g \cdot L^{-1}$	Δ14	Δ7
7	40.3	7.1	−11.0**	4	24.2	−0.1	1.4	7	3.3	−0.5	−0.6
ns	34.3	−9.5	−8.6	ns	22.2	−0.8	−1.6	ns	2.5	−0.2	−0.1
ns	18.1	3.3	3.4	ns	22.0	−1.7	−1.5	10	2.9	−0.4	−0.6

25.1 $mg \cdot 100\ mL^{-1}$ in winter, 24.1 $mg \cdot 100\ mL^{-1}$ in spring, and 19.0 $mg \cdot 100\ mL^{-1}$ in summer; 45% of the variation was explained by CI and GSI. In winter, because plasma glucose was rising in the last days of the experiment (Fig. 4), a better estimate of its seasonal value could be obtained by considering only the last day, i.e., after apparent recuperation to normal values, with a concentration of 37.0 $mg \cdot 100\ mL^{-1}$.

Seasonality in plasma protein concentrations was high (27.9); concentrations varied from 17.3 to 23.0 $g \cdot L^{-1}$, with spring and summer showing the highest values. Ninety percent of this variation was explained by the interaction between season and WT or CI. The average (SE) GSI of the plaice was higher in winter, 2.29 (0.14) and spring, 2.50 (0.24), than in summer, 1.25 (0.06) and fall, 1.39 (0.02). The CI of fish was similar in summer, fall, and winter (1.04 (0.02)) and higher in spring (1.09 (0.01)).

Response to Transfer

MCHC, blood hemoglobin, plasma protein, potassium, and glucose showed large amplitude in the initial response to transfer and great similarity between all treatments in the overall temporal response, these characteristics being more pronounced in fall and winter. The winter response was chosen for more detailed examination (Fig. 4), because the temperature in this season was stable throughout the experiment (Fig. 1). Plasma potassium was not shown in Fig. 4, its fluctuations being well represented by MCHC.

Temporal dependence was confirmed by general linear model analyses, where significant proportions of total variance associated with the day varied between 0.11 and 0.26 among plasma proteins, plasma potassium, plasma glucose, blood hemoglobin, and MCHC. Association of these variables with the covariables WT, CI, and GSI remained below 0.10 in all except plasma proteins (0.50). Three patterns of temporal variation in concentrations were seen (Fig. 4). Plasma protein and blood hemoglobin concentrations showed distinct peaks on day 3 or day 4 (28 $g \cdot L^{-1}$ and 4 $g \cdot 100\ mL^{-1}$, respectively), then decreased and stabilized more or less after day 7 (16 $g \cdot L^{-1}$ and 2.5 $g \cdot 100\ mL^{-1}$, respectively). MCHC (Fig. 4) was higher around day 3 or day 4 (25 $g \cdot 100\ mL^{-1}$), decreased from day 7 to day 14, and increased or remained stable from day 21 to day 28. Plasma glucose concentrations decreased from day 1 to day 7, then steadily increased to day 28, ranging from 10 to 35 $mg \cdot 100\ mL^{-1}$. Thus, for these variables, concentrations went through a minimum then increased back to levels similar to or approaching that of untransferred controls.

The similarity in the temporal patterns of the different variables in Fig. 4 suggests a reaction to a common underlying factor that, in the present case, could be the transfer process because fish from all salinity treatments showed the same reaction. The results of the principal components analysis also suggest a common reaction of blood hemoglobin, hematocrit, MCHC, plasma glucose, plasma proteins, plasma potassium, and plasma cortisol by connecting all of them as important contributors to factor 3. The only variable among those that did not show consistent time fluctuations in winter was plasma cortisol, because of an interaction with salinity. Mean plasma cortisol concentrations remained generally low with 89% of the concentrations below 10 $\mu g \cdot 100\ mL^{-1}$.

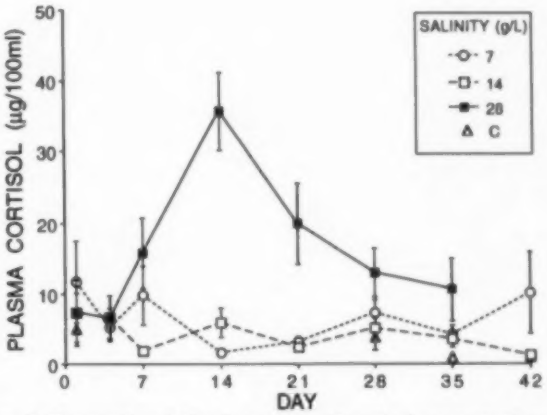

FIG. 3. Temporal variation in summer of cortisol concentrations in plaice transferred directly from 28 $g \cdot L^{-1}$ to 7, 14, and 28 $g \cdot L^{-1}$ salinity and in fish not transferred (C: 28 $g \cdot L^{-1}$). Each point represents the mean value ± SE (n = 10). Plaice transferred to 28 $g \cdot L^{-1}$ were sick while the others were not.

Transfer may also have induced osmo-ionic variations. In Fig. 1 one can note peaks or troughs in the plasma sodium concentrations during the first 7 d, which are similar to the initial reactions described in Fig. 4. However, this osmotic reaction to transfer shows a smaller scale than the osmotic reaction to the salinity treatment, especially at 7 $g \cdot L^{-1}$ *S*. Conversely, the reaction to salinity may have affected the transfer response because, over the whole experimental period, the plasma glucose concentrations were significantly lower at 7 $g \cdot L^{-1}$ than at 21 $g \cdot L^{-1}$ in fall and than at 21 and 28 $g \cdot L^{-1}$ in winter.

Discussion

There were no mortalities of American plaice transferred to salinities at or above 7 $g \cdot L^{-1}$ in fall, winter, and summer

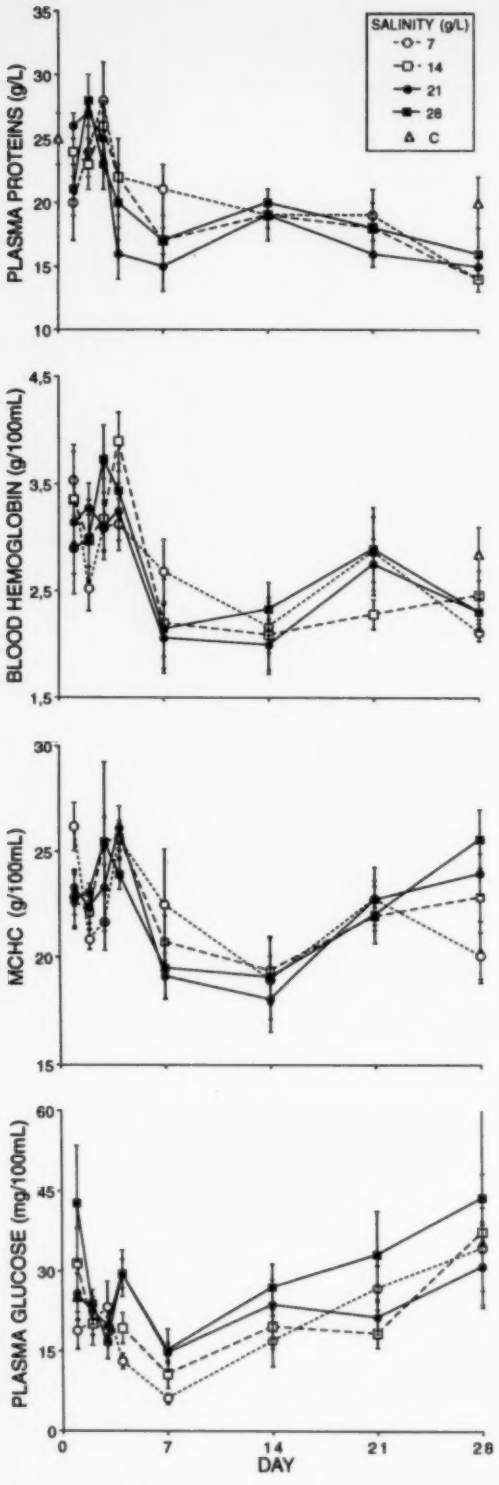

FIG. 4. Temporal variations in winter of plasma protein concentration, blood hemoglobin, mean cellular hemoglobin content (MCHC), and plasma glucose in plaice transferred directly from 28 $g \cdot L^{-1}$ to 7, 14, 21, and 28 $g \cdot L^{-1}$ salinity and in fish not transferred (C: 28 $g \cdot L^{-1}$). Each point represents the mean value ± SE (n = 10).

but none survived in fresh water in any season. Dutil et al. (1992) found a similar pattern of survival in Atlantic cod exposed to similar salinity and Provencher et al. (1993) further defined the resistance limit of cod as between 3 and 5 $g \cdot L^{-1}$. In the Gulf of St. Lawrence, American plaice are found at temperatures between −1 and 6°C, from depths of 75 m in summer to 350 m in winter (Powles 1965), and where salinity varies from 32 to 34 $g \cdot L^{-1}$ (Koutitonsky and Bugden 1991). On the Scotian Shelf, preferred temperatures vary from 1 to 9°C (Scott 1982). Our results suggest that, like Atlantic cod, American plaice is more tolerant of low salinities than what would be expected from the characteristics of its habitat. This does not seem to be uncommon in marine species. High tolerance to low salinities was shown in red grouper (*Epinephelus akaara*) and black sea bream (*Mylio macrocephalus*), with survival at 5 $g \cdot L^{-1}$ and 3 $g \cdot L^{-1}$, respectively (Woo and Wu 1982), and Wu and Woo (1983) demonstrated that the LD_{50} limit was close to 7 $g \cdot L^{-1}$ in seven coastal or deepwater marine species.

From the results of plasma sodium concentrations and muscle water content at the end of the experimental periods, we can summarize the osmotic response as absent following transfers to 28 and 21 $g \cdot L^{-1}$, minor at 14 $g \cdot L^{-1}$, and pronounced at 7 $g \cdot L^{-1}$ *S*. At 7 $g \cdot L^{-1}$ *S*, plasma sodium concentration dropped abruptly for 14–21 d and then stabilized at its lowest level, between 115 and 125 $mmol \cdot L^{-1}$. This represents a difference of 42–52 $mmol \cdot L^{-1}$ from the control. In contrast, Atlantic cod transferred to 7 $g \cdot L^{-1}$ under similar experimental conditions also showed a strong decline in plasma sodium concentrations, but those were partially restored in 14 d to concentrations 20 $mmol \cdot L^{-1}$ below controls (Dutil et al. 1992). Provencher et al. (1993) demonstrated a response in cod transferred to 3 $g \cdot L^{-1}$ similar to that in plaice transferred to 7 $g \cdot L^{-1}$, with a new steady state of plasma sodium being reached around 100–120 $mmol \cdot L^{-1}$. In both species, these low levels of plasma sodium were interpreted as partial failure to cope with the low-salinity conditions. This is supported in cod by a 50% mortality rate following exposure to 3 $g \cdot L^{-1}$ (Provencher et al. 1993) and in plaice by high plasma cortisol concentrations at 7 $g \cdot L^{-1}$ in winter and summer. Moreover, Berthiaume et al. (1993) found a significant increase of lymphocystis tumors in American plaice at 7 $g \cdot L^{-1}$. They postulated that the presence of physiological stress under low-salinity conditions could have reactivated a latent virus.

Arnold-Reed and Balment (1991) observed lower plasma sodium concentrations in summer compared with winter in a 13-d freshwater transfer experiment with European flounder (*Platichthys flesus*). They interpreted this reaction as an enhanced ability to adjust to a wider range of salinity in summer. This species is considered euryhaline, because a study by Vislie and Fugelli (1984) showed little or no swelling of cells (considered as a criterion of euryhalinity (Florkin and Schoffeniels 1969)) for a period of 6 d following transfer from seawater to freshwater despite a 50 $mmol \cdot L^{-1}$ decrease in plasma osmolality. In a fall seawater–freshwater transfer experiment, done on the same species by Nonnotte and Truchot (1990), a 33-d follow-up revealed a recovery to plasma sodium values 10 $mmol \cdot L^{-1}$ below the control.

Similarly, in the experiment of Arnold-Reed and Balment (1991), plasma sodium level was low in summer but returned to values close to the controls, although recovery was still incomplete after 14 d. In view of this recovery phenomenon in an adaptable species, low plasma sodium concentrations would indicate a lack of control rather than a better capacity to acclimate to fresh water. Our studies on Atlantic cod (Dutil et al. 1992) and American plaice suggest that acclimation to low salinities in marine species is related to the ability to maintain plasma osmolality at levels closest to those observed in seawater. In contrast, truly euryhaline species such as banded killifish (*Fundulus diaphanus*) adjust their plasma osmotic pressure to lower levels in fresh water than in seawater, without apparent indications of stress (Ahokas and Duerr 1975). In American plaice transferred to 7 $g \cdot L^{-1}$, the muscle water content increased by 2.0–3.3%. If this represents mostly cellular water, as suggested by the study of Vislie and Fugelli (1984), the increase of muscle water content above the 1% maximum increase observed in freshwater transferred European flounder may indicate stress in plaice at this salinity.

Stress condition associated with transfer of American plaice from 28 to 7 $g \cdot L^{-1}$ varied from one season to another. Cortisol concentrations at 7 $g \cdot L^{-1}$ were intermediate in summer and winter, i.e., below the concentrations observed in sick fish at 28 $g \cdot L^{-1}$ in summer, but above all the others measured in this study. There was no difference in plasma cortisol concentrations between salinities in the other two seasons. Summer is characterized by elevated temperature and gonad maturation, variables that could decrease the fish's ability to osmoregulate under less favourable conditions. In Atlantic cod kept at 28 $g \cdot L^{-1}$, Audet et al. (1993) demonstrated a relationship between plasma sodium concentration and temperature, but were unable to demonstrate such a relationship in American plaice. However, the present study of 14 $g \cdot L^{-1}$ indicated lower plasma sodium concentration in summer compared with the other seasons and indicated a combined effect of elevated temperature with low salinity. An intermediate graded effect of salinity was also observed in muscle water and a small effect on plasma potassium, glucose, and hematological variables used as secondary stress indicators. This suggests that osmotic adjustment at the different salinities was not associated with major metabolic changes and did not generally produce high stress levels in fish.

At all salinities, MCHC, blood hemoglobin, plasma protein, plasma potassium, and plasma glucose featured marked fluctuations in fall and winter. Because these variations were in phase and of similar intensity among salinities, they were regarded as a common response to transfer and sampling in these two seasons. Plasma glucose showed a 65% decrease from day 1 to day 7, suggesting a decrease in glucose reserves, and returned to levels similar to controls after 28 d. Confinement in nets or forced exercise repeated at daily intervals in tank-adapted marine plaice (*Pleuronectes platessa*; Wardle 1972) and European flounder (Waring et al. 1992) induced an increase of less than 40% followed by a return to normal values within 24 h. In Atlantic cod, transfer and sampling disturbance at less than daily intervals were characterized by a regular decrease in plasma glucose (Provencher et al. 1993). It is, thus, possible that our daily sampling schedule in the first week induced cumulative stress, which was alleviated when weekly sampling started on day 7. However, stress from transfer and sampling may have been undetected by measuring cortisol levels. The 24-h period of increased cortisol that was observed in physically stressed European flounder (Waring et al. 1992) is shorter than our daily sampling schedule. An increase in plasma proteins characterized the initial response to salinity transfers. After 3–4 d, protein concentration decreased and stabilized at values somewhat below those in untransferred controls. A similar response was shown for blood hemoglobin, although delayed in time, which may explain the low proportion of variation associated with the plasma protein concentration. The changes in hematological parameters and plasma potassium, which occur just after changes in plasma protein concentration, are also indicative of a secondary stress response (Mazeaud et al. 1977; Thomas 1990). Plasma protein and potassium concentrations have been shown to respond strongly to physical disturbance in European flounder (Waring et al. 1992).

Seasonal effects were studied with the 14 $g \cdot L^{-1}$ transfer experiments. In most cases, the results confirmed the seasonal variations observed by Audet et al. (1993) at 28 $g \cdot L^{-1}$. At 14 $g \cdot L^{-1}$, the seasonal effect was minimal in terms of plasma sodium response (156–164 $mmol \cdot L^{-1}$), but extensive for plasma potassium (2.8–4.0 $mmol \cdot L^{-1}$). These ions varied in opposite ways, with plasma potassium at its maximum in summer when plasma sodium reached its lowest values; these changes have been discussed by Audet et al. (1993). However, the present study showed seasonal differences in terms of the intensity of the glucose response associated with transfer and sampling stress. In fall and winter, plasma glucose showed a similar response following all salinity transfers, with high initial and final levels, whereas the spring and summer concentrations were always low. Combined with the possibility of a cumulative sampling effect as discussed before, this seasonal variation was related to the GSI. The presence of the highest GSI in spring and the lowest in summer is similar to what has been found in American plaice sampled on the Atlantic coast by MacKinnon (1972), who showed a maximum of energy stored in fall and winter and a minimum in spring and summer. This would suggest depleted glycogen stores in spring and summer and would explain the absence of glucose response following tank transfer in these seasons.

In conclusion, the American plaice can withstand salinities down to concentrations of 14 $g \cdot L^{-1}$ with only slight variations in the osmo-ionic blood condition. It can also tolerate salinities as low as 7 $g \cdot L^{-1}$ with a new adjustment of its osmotic balance. No indication of stress or increased energy expenditure was revealed at salinities between 28 and 14 $g \cdot L^{-1}$. At 7 $g \cdot L^{-1}$, however, one cannot be certain of the complete absence of chronic stress, as suggested by some intermediate values of cortisol at this salinity. In a recent report, Sinclair (1993) described a very alarming situation for some American plaice stocks. Some have declined to extremely low level and a much-reduced fishery is expected. Aquaculture of groundfish species could be a valuable option to provide, at least, some of the market needs. It is, therefore, recommended that if American plaice is to be grown in estuarine waters, care should be taken that salinity concentration does not drop below a safe limit of 14 $g \cdot L^{-1}$.

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A 6-Yr Record of Nutrient Element Sedimentation and Recycling in Three North Temperate Lakes

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Sedimentation of C, N, and P from the water column was assessed during the ice-free seasons of 1986–91 in three northern Wisconsin lakes. Seasonal trends in mass sedimentation were different among lakes but consistent from year to year within each lake. High rates of nutrient sedimentation were associated with spring and fall blooms of large siliceous algae. Nutrient recycling, calculated as the difference between uptake during photosynthesis and loss to sedimentation, showed seasonal trends that were related to sedimentation. Recycling within the water column was the most important source of nutrients to primary producers, accounting for 85–90% of P demand during the summer stratified period.

La sédimentation du C, du N et du P dans la colonne d'eau a été évaluée durant la saison sans glace dans trois lacs du nord du Wisconsin de 1986 à 1991. Les tendances saisonnières de la sédimentation étaient différentes dans chacun lac, mais elles étaient constantes d'une année à l'autre dans chacun des lacs. Les taux élevés de sédimentation des nutriments étaient liés à l'efflorescence printanière et automnale des grandes algues siliceuses. Le recyclage des nutriments, calculé comme la différence entre la captation effectuée pendant la photosynthèse et la perte due à la sédimentation, a montré des tendances saisonnières qui étaient liées à la sédimentation. Le recyclage dans la colonne d'eau constituait la plus importante source de nutriments pour les producteurs primaires et comptait pour 85–90% de la demande en P durant la période de stratification estivale.

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Nutrient-element loading and internal recycling play key roles in controlling primary production and water quality in lakes (Lean et al. 1987; Scavia and Fahnenstiel 1987; Caraco et al. 1992). Regulation of nutrient loading or availability is often a major component of water quality management programs (Gächter and Imboden 1985). Thus, an understanding of the factors controlling the fluxes of available nutrient elements to the photic zone of lakes from both internal and external sources is needed.

Sedimentation of particles from the water column to the bottom sediments of lakes is an important removal mechanism for biologically essential elements (Smith et al. 1989; Caraco et al. 1988; Sigg 1985; Bloesch et al. 1977) and, thus, influences nutrient-limited production in lakes. Nutrient sedimentation can be assessed with sediment traps, which integrate all processes affecting particle formation and deposition over the time period of trap deployment. Additionally, sediment traps provide information on seasonal trends in particle deposition that are not apparent from analysis of benthic sediment cores.

Recycling is a potentially important source of nutrients to primary producers (Bloesch et al. 1977; Caraco et al. 1992; Poister 1992). Bacteria and zooplankton transform biologically occluded nutrients to dissolved forms used by primary producers (Berman 1970; Rigler 1973; Lehman 1980; Ammerman and Azam 1985). Fish also excrete dissolved nutrients (Carpenter et al. 1992; Schindler et al. 1993; Kraft 1993). To assess the net effect of recycling on nutrient availability, an approach that considers all possible recycling pathways is required.

The Northern Temperate Lakes site of the National Science Foundation sponsored Long Term Ecological Research (LTER) program (Magnuson et al. 1984) has provided an opportunity to evaluate nutrient recycling over several annual cycles. Six years of primary-production measurements (Adams et al. 1993) enable calculation of nutrient-element demand while concurrent sediment-trap deployments provide a measure of nutrient loss from the water column by sedimentation. Recycling of a given nutrient element in the water column can be estimated by combining measurements of demand and loss. This mass-balance approach combines the effects of individual recycling mechanisms in one term.

This paper is concerned with two aspects of the nutrient cycle: sedimentation and recycling. First, we discern seasonal and interlake trends in mass sedimentation rates. An explanation for the observed trends involving increased sedimentation by siliceous algae is discussed. C, N, and P sedimentation from the water column is also assessed. We

TABLE 1. Important chemical, biological, and physical characteristics of Crystal, Sparkling, and Trout (south basin) lakes, Vilas County, Wisconsin. Data are from LTER North Temperate Lakes database, Dr. Barbara Benson, Data Manager, Center for Limnology, University of Wisconsin-Madison, 680 North Park Street, Madison, WI 53706, USA. All variables are averages of data collected from the entire water column and throughout the year from 1982–91 except where noted.

	Crystal	Sparkling	Trout
Surface area (km^2)	0.37	0.81	11
Maximum depth (m)	20.4	20.0	35.7
Summer Secchi depth (m)	9	6	5
Primary production, 1986–90 ($mg\ C \cdot m^{-2} \cdot d^{-1}$)	729	585	569
Alkalinity (μequiv./L)	14	608	826
pH	6.0	7.3	7.4
Specific conductance (μS/cm)	14	77	91
Total phosphorus (μg/L)	6.4	12	10
Water column PBSI 1982[a] (μg/g particles)	24	56	63
Total particulate matter (mg/L)	0.62	0.85	0.85

[a]Hurley (1984).

discuss how biotic factors, such as phytoplankton nutrient rations, and abiotic factors, such as Fe-associated P sedimentation, influence nutrient removal from the water column. Secondly, we evaluate the relation between nutrient element sedimentation and recycling in the water column and the importance of recycling as a P source to primary producers.

Site Description

Crystal, Sparkling, and Trout lakes are located within a common groundwater flow system in Vilas County, Wisconsin. Crystal Lake receives approximately 10% of its annual water inflow from groundwater with the remaining 90% from precipitation (Hurley et al. 1985; Kenoyer 1986). Groundwater contributes approximately 25% of the annual water inflow to Sparkling Lake, with the balance of the budget coming from precipitation (Krabbenhoft 1988; Krabbenhoft et al. 1990). The hydrologic budget for Trout Lake is more complicated. Trout Lake, located at the bottom of the groundwater flow system, probably receives more groundwater than either Crystal Lake or Sparkling Lake. In addition to precipitation and groundwater, Trout Lake receives surface water from four small tributaries and discharges through one outflowing stream. Differences in the morphometry and hydrology influence the chemical and biological composition of the three study lakes (see Table 1).

Crystal, Sparkling, and Trout lakes represent a gradient of the proportion of siliceous algae in the phytoplankton community. Diatom abundance is an important lake characteristic in relation to sedimentation, because diatoms have a higher sinking velocity than other major phytoplankton groups (Reynolds et al. 1982; Reynolds and Wiseman 1982). Diatoms comprise a significant portion of the phytoplankton of Trout Lake throughout the ice-free season, along with other chrysophytes, green and blue-green algae, and dinoflagellates (Lay 1985). Carotenoid pigments common to diatoms (fucoxanthin, diadinoxanthin, and diatoxanthin) represent 70–80% of the total carotenoid flux to sediment traps in Trout Lake (Hurley 1988; Hurley and Armstrong 1991). Sparkling Lake pigments also reflect diatom production supported by high silicon concentration (Hurley 1988). A strong positive relationship between particulate biogenic silica and chlorophyll *a* concentration shows that siliceous algae also make up a significant portion of the phytoplankton community in Crystal Lake (Hurley et al. 1985). Because the three lakes are fairly similar in respect to annual areal primary productivity, differences in silica concentration (Table 1) suggest that the interlake trend with respect to production of siliceous algae as a percentage of total production is Trout > Sparkling > Crystal. Interlake differences in the C/Si molar ratio of the suspended particulate matter also reflect the interlake trend in siliceous algae production. The molar C/Si ratios for samples collected throughout the year in 1982 were 7.7, 11.4, and 26.1 for Trout, Sparkling, and Crystal lakes, respectively (Hurley 1984).

Methods

Sediment traps were deployed in Crystal, Sparkling, and Trout lakes throughout the ice-free season from 1986 to 1991. Two traps poisoned with 0.2 g NaN_3 were deployed 3–5 m apart in each lake. NaN_3 was used to retard microbial decomposition of the trap material while minimizing swimmer poisoning (Lee et al. 1992). The cylindrical traps were 44 cm tall with a collection area of 165 cm^2. The conical trap bottom collected sedimenting particles in a detachable plastic bottle. At approximately 4-wk intervals, trap material was collected and the traps were redeployed with new bottles and poison. The traps were anchored in the deep hole of each lake approximately 7 m from the sediment–water interface of Sparkling and Crystal lakes and 8–13 m from the sediment–water interface of Trout Lake.

Trap material from each interval was size fractionated using a nylon macroporous sieve. From 1986 through 1988, a 111-μm mesh size was used. In 1989 the mesh size was

changed to 210 μm to better separate zooplankton from large phytoplankton. Mass flux for each fraction was determined by filtering a subsample through a preweighed 0.4-μm pore size polycarbonate Nuclepore filter.

Trap material from each size fraction was freeze-dried and analyzed for nutrient concentration. Total C and N were determined with a Perkin-Elmer 240c Elemental Analyzer. In earlier work, the coefficients of variation obtained using the same instrument were 2.7% for C and 7.1% for N (Fullerton 1988). Total P was determined by digestion of 10–20 mg of trap material with perchloric–nitric acid (Sommers and Nelson 1972) and subsequent molybdate blue determination of phosphate concentration in the digest (Murphy and Riley 1962). A 95% confidence interval for phosphorus concentration (percentage of sediment mass) was estimated at ±3%, based on 16 replicates of one sample analyzed during five different digestion runs. The accuracy of this method was assessed by analyzing a National Bureau of Standards (NBS) reference material (No. 1646, estuarine sediment). The average percent P by weight was determined to be 0.0582 ± 0.0077 (95% confidence interval) compared with 0.054 ± 0.005 determined by NBS.

Nutrient sedimentation was calculated by multiplying mass flux to the sediment trap ($mg \cdot m^{-2} \cdot d^{-1}$; see Fig. 1) by nutrient concentration (mg nutrient/mg sediment) to give nutrient flux (mg nutrient $\cdot m^{-2} \cdot d^{-1}$).

Nutrient fixation was obtained from measured inorganic carbon incorporation during photosynthesis using the ^{14}C technique (Adams et al. 1990) and average molar C:N:P ratios of standing particulate matter, measured during the 1982 ice-free season. The C/N ratios were 9.5, 9.4, and 10.4 and the C/P ratios were 223, 297, and 164 for Crystal, Sparkling, and Trout lakes, respectively (Hurley 1984). Daily inorganic carbon fixation was calculated by using semiweekly ^{14}C incubations of water-column samples at various light intensities in conjunction with water-column light profiles and daily surface-light measurements (Adams et al. 1990). The resulting daily incorporation-rate estimates (mg nutrient $\cdot m^{-2} \cdot d^{-1}$) were averaged over the period of sediment-trap deployment. Two important assumptions are made in the calculation of nutrient fixation: (1) the incorporation of inorganic carbon calculated by the ^{14}C uptake method is assumed to correspond to the amount of carbon converted to photosynthetic biomass in the natural environment; (2) the ratios of C:N:P used to calculate N and P incorporation are assumed to remain constant throughout the ice-free season. The latter is an important assumption because uncertainty in nutrient ratios can significantly affect mass-balance calculations of nutrient regeneration (McCormick and Tarapchak 1984).

Total particulate matter was measured at four or five depths in each lake on or near the day of trap deployment. Lake water samples were pumped through an in-line, preweighed 0.45-μm pore size polycarbonate filter. Particulate nutrient concentrations were measured throughout the ice-free season in 1982 (Hurley 1984). Mean nutrient concentrations (mg/mg) for Crystal, Sparkling, and Trout lakes, respectively were C: 318, 306, and 247; N: 39, 39, and 27; P: 3.7, 2.7, and 3.9. Changes in the standing stock of particulate nutrients were calculated as the product of the change in particle concentration ($mg \cdot m^{-2} \cdot d^{-1}$) over the interval of trap deployment and particulate-nutrient concentration (mg/mg).

Results and Discussion

Particulate Matter Sedimentation

Seasonal trends in the flux of particulate matter to sediment traps are varied from lake to lake but fairly consistent from year to year within each lake (Fig. 1). The mass sedimentation flux in Trout Lake is relatively high in both spring and fall. Sparkling Lake shows a modest sedimentation maximum in spring and higher maximum in fall. The flux in Crystal Lake increases throughout the summer and is variable from year to year.

The spring sedimentation maximum may result from deposition of material produced through primary production (as measured by ^{14}C uptake; Fig. 2). In all three lakes, primary-production peaks in early summer at periods corresponding roughly to the spring sedimentation maxima in Sparkling and Trout lakes. However, sedimentation does not mirror production. In Sparkling Lake, the spring sedimentation maximum is small, even though this lake has the highest early summer peak in primary production of the three lakes studied. High early summer production in Crystal Lake does not result in rapid algal sedimentation.

The effect of the spring production maximum on sedimentation is related to both the qualitative and quantitative aspects of production. The coincidence of periods of high production and high particulate biogenic silica concentration indicates spring production maxima are caused by blooms of diatoms and other siliceous algae (Hurley 1984). The contribution to sedimentation relative to production tends to be high for certain common diatoms, which have higher sinking rates than other phytoplankton (Reynolds and Wiseman 1982). Thus, seasonal trends in mass sedimentation in Crystal, Sparkling, and Trout lakes are apparently influenced by sedimentation of large siliceous algae. The pigment content of trap material from Sparkling and Trout lakes also reflects increased diatom sedimentation during periods of increased mass sedimentation (see Fig. 1); deposition of diatom-related pigments is high in spring and fall in Trout Lake and in fall in Sparkling Lake (Hurley 1988; Hurley and Armstrong 1991). Spring blooms of siliceous algae in Crystal and Sparkling lakes generally do not result in high mass sedimentation during spring and early summer, indicating that these blooms are comprised of smaller, slowly sinking siliceous algae. The smaller algae are decomposed and grazed in the water column for longer periods, decreasing sedimentation. Biomanipulation experiments in limnocorrals indicate that trends in particle sedimentation are usually controlled by the net phytoplankton community, while smaller plankton have less effect on sedimentation (Bloesch and Bürgi 1989).

In addition to seasonal trends in mass sedimentation, interlake differences are significant. Mass fluxes during the summer stratified period for Crystal, Sparkling, and Trout lakes, averaged over the 6-yr period, are 269, 246, and 413 $mg \cdot m^{-2} \cdot d^{-1}$, respectively. The stratified-period flux is significantly higher in Trout Lake than in both Crystal ($p = 0.012$, two-sided t-test) and Sparkling lakes ($p = 0.0014$). When the entire ice-free season is averaged, the difference between Trout and the other two lakes is larger and the interlake trend in mass flux becomes: Trout > Sparkling > Crystal. Interlake differences cannot be attributed to differences in biomass production through photosynthesis

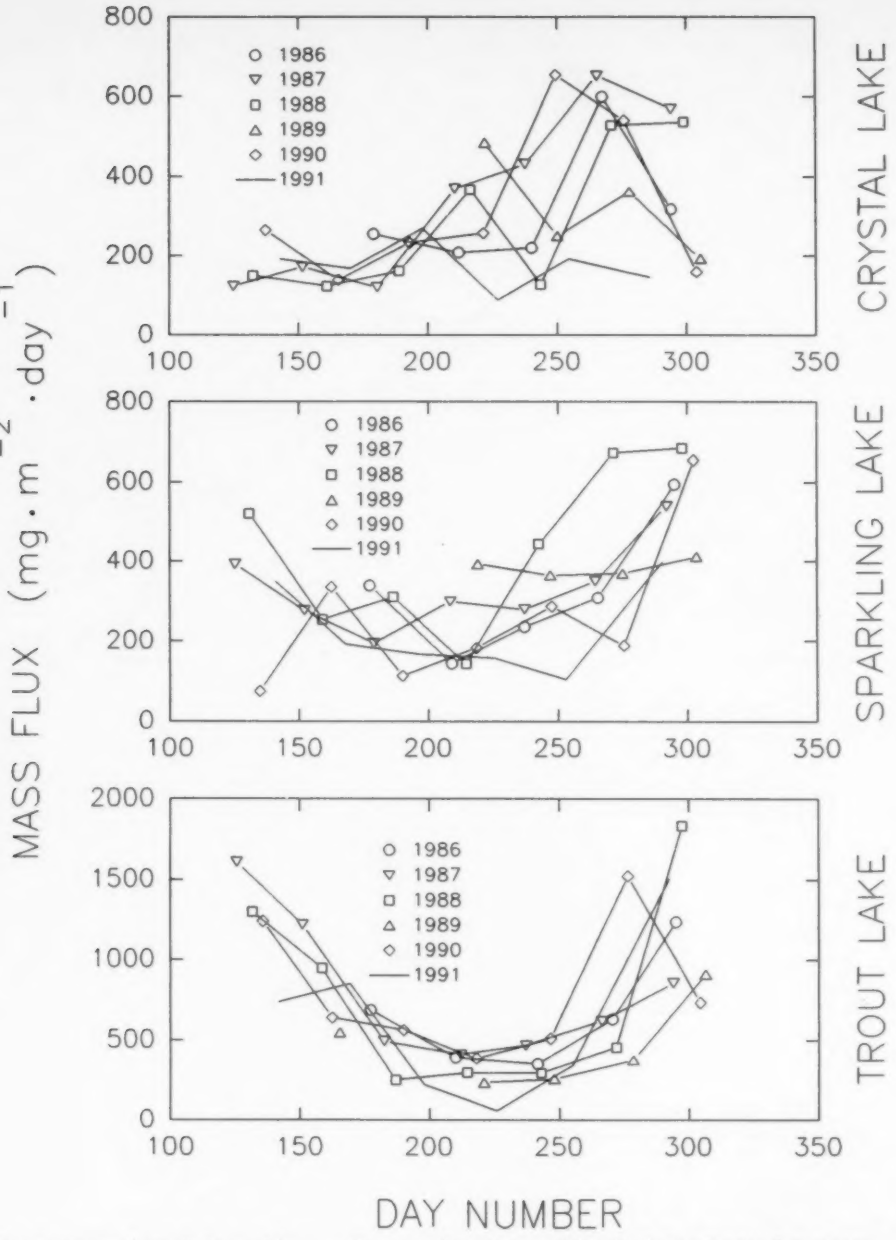

FIG. 1. Seasonal trends in particle mass flux to sediment traps 1986–91 during the ice-free season.

because the interlake trend in mass sedimentation is opposite to the trend in areal primarily production: Crystal > Sparkling > Trout (Table 1). Sedimentation of siliceous algae may also be responsible for the observed interlake mass sedimentation trend. Based on particulate biogenic silica concentrations and molar C/Si ratios, the interlake trend in proportion of siliceous algae appears to be: Trout > Sparkling > Crystal. Furthermore, conversion of particulate biogenic silica (Table 1) to biomass (Shafer 1988) indicates that siliceous algal mass averages about 9, 20, and 22% of the total areal particulate matter in Crystal, Sparkling, and Trout lakes, respectively. Thus, we attribute seasonal and interlake trends in sedimentation to high sedimentation rates of siliceous algae. In addition, differences in production of siliceous algae apparently cause the mass sedimentation trend among lakes to be opposite that which is expected based on the relative primary productivity of these lakes.

Sediment-trap material was not analyzed for silica content during our main study period (1986–91), but biogenic silica was measured from traps deployed in 1982 (Hurley 1984). Silica deposition in 1982 showed spring and fall maxima in Sparkling and Trout lakes and a gradual increase

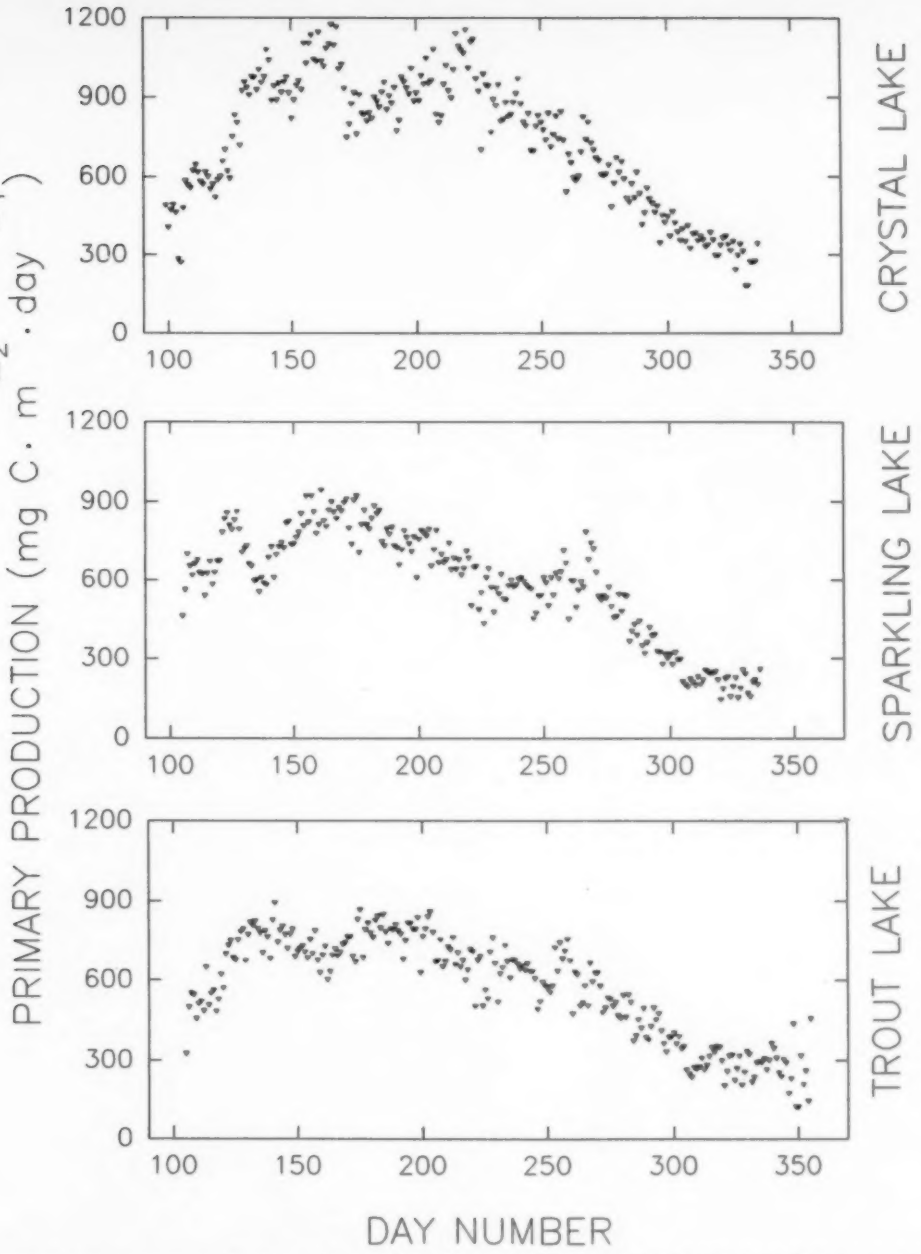

FIG. 2. Average daily primary production estimates 1986–90 based on biweekly ^{14}C incubations (Adams et al. 1990).

throughout the summer in Crystal Lake. The seasonal trends in sedimentation of biogenic silica and particulate matter are similar to each other. In addition, the interlake trend in average annual silica deposition (Trout > Sparkling > Crystal) is the same as the interlake trend in mass flux to sediment traps. Trends in 1982 silica deposition correspond to trends in mass sedimentation from 1986 to 1991 and support the conclusion that sedimentation of siliceous algae influences mass sedimentation in these lakes. Seasonal patterns of mass flux are remarkably similar from year to year in these systems (Fig. 1). Therefore, we believe comparison of 1986–91 data to the silica content of sediment trap material in 1982 is appropriate.

In summary, seasonal and interlake differences in mass sedimentation in Crystal, Sparkling, and Trout lakes are distinct and consistent from year to year and appear to be influenced by the sedimentation of siliceous algae. We have considered other possible sources of the observed sedimentation trends such as overtrapping due to turbulence, redeposition of benthic particles, swimmer poisoning, zooplankton fecal

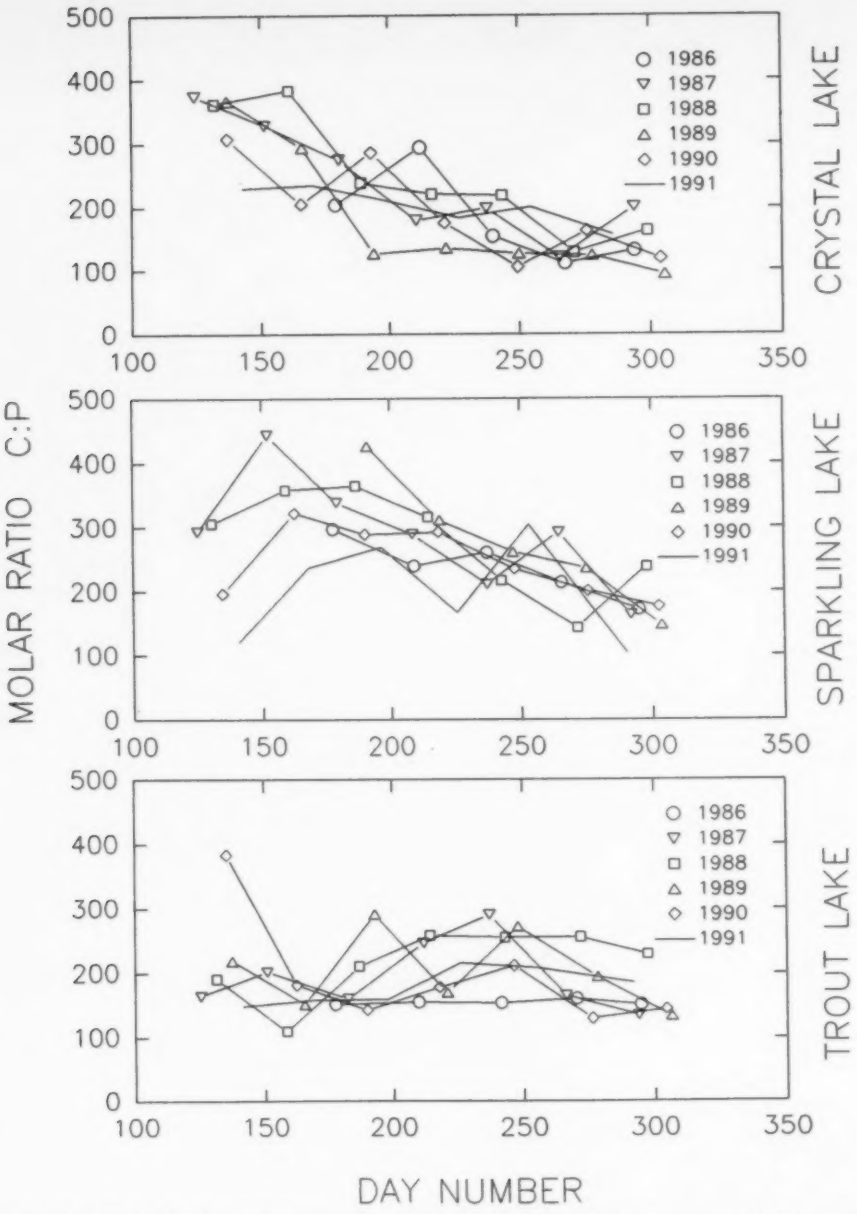

FIG. 3. C/P molar ratio of small size fraction sediment trap material 1986–90 during the ice-free season. (<111 μm for 1986–88; <210 μm for 1989–91).

pellet deposition, and input of allochthonous particulates, and conclude that these factors do not greatly influence trends in sedimentation (Poister 1992).

Nutrient Element Sedimentation

To quantify the removal of essential nutrient elements from the water column through sedimentation, concentrations of C, N, and P in trap material were measured. Nutrient ratios in the smaller size fraction of trap material show consistent seasonal trends from year to year (Fig. 3). The C/P molar ratios in Crystal and Sparkling lakes decreased gradually throughout the summer owing to an increase in the P content of the trap material. In contrast, the C/P ratio of the smaller size fraction in Trout Lake remained fairly constant throughout the summer. Seasonal trends were not apparent in the larger size fraction (Poister 1992). However, the average C/P molar ratio is significantly lower in the smaller than in the larger size fraction (Table 2), reflecting differences in types of particles in the two size fractions. Zooplankton carapaces, which comprise most of the larger size fraction of trap material, generally have a C/P molar ratio higher than algae and fecal matter in the smaller size

TABLE 2. Comparison of nutrient ratios (molar C/P and C/N) for Crystal, Sparkling, and Trout lakes. The p values are the probability that the molar ratios of the larger and smaller size fractions are equal as determined by a paired t-test. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$; ns, not significant ($p \geq 0.05$).

Lake	Size fraction (μm)	C/P	C/N
Crystal	<111	225*	7.50^{ns}
	>111	257	6.83
	<210	192***	9.17^{ns}
	>210	355	7.26
Sparkling	<111	271*	8.24^{ns}
	>111	473	7.87
	<210	238***	9.10^{ns}
	>210	425	8.61
Trout	<111	192**	8.83*
	>111	278	6.91
	<210	194**	10.0^{ns}
	>210	339	9.24

fractions. The C/N molar ratio does not show seasonal trends (Poister 1992) or significant differences between lakes or size fractions collected by the same trap (Table 2).

C/P ratios of sediment-trap material differ significantly among lakes. The C/P ratio of the smaller size fraction is higher in Sparkling than in Crystal Lake or Trout Lake. If we assume most trap material in the smaller size fraction is algal remains, the lower C/P ratio in Trout Lake implies that phytoplankton in this lake are less P deficient than in the other two lakes (Healey and Hendzel 1979, 1980; Tezuka 1985); this is consistent with the fact that Trout Lake receives more surface-water and groundwater input than the other two lakes. The C/P molar ratio of suspended particulate matter collected during the ice-free season of 1982 showed the same trend among lakes as the trap material (Sparkling > Crystal > Trout; Hurley 1984).

In addition to settling plankton, seasonal trends in the C/P molar ratio of sediment-trap material reflect the influence of another internal lake process, sedimentation of iron (III) oxyhydroxides. Throughout the stratified period, the hypolimnia of these lakes become increasingly anoxic, especially in Sparkling Lake (Poister 1992). Anoxic hypolimnia above benthic sediments containing Fe can lead to increased P sedimentation via the "ferrous wheel" (Campbell and Torgersen 1980). This mechanism scavenges biologically available P on iron oxyhydroxide particles that eventually sediment out of the water column (Mayer et al. 1982; Tessenow 1974). This link between P and Fe sedimentation and accumulation is common among lakes in this region (Williams et al. 1971).

Interlake and seasonal trends in the molar C/P ratios of sedimenting particles in our study lakes (Fig. 3) reflect the influence of Fe-associated P sedimentation. Although probably contributing to P sedimentation in Trout Lake, the influence of the "ferrous wheel" on the seasonal trend in the C/P molar ratio of trap material is less obvious than in Sparkling and Crystal lakes. In Trout Lake, the total P sedimentation flux is larger than in Crystal and Sparkling lakes, and the Fe-associated P flux comprises a smaller proportion of the total.

TABLE 3. Nutrient ratios of sediment-trap material in the three study lakes and percent difference from Redifield molar ratios (106:16:1; Redfield et al. 1963). Ratios reported for each lake represent an average of all size fractions from 1986–91.

	Crystal		Sparkling		Trout	
	C/P	C/N	C/P	C/N	C/P	C/N
Average ratio	257	7.70	352	8.43	250	8.75
% difference	142	16	232	27	126	32

Fe-associated P sedimentation may also contribute to the significantly lower C/P ratio of the smaller size fraction as compared to the larger size fraction (Table 2). Fe-bound phosphates are found mostly in the smaller size fraction.

More detailed work on 1982 samples (Hurley 1984) provides direct evidence for the influence of Fe on the seasonal trends in P sedimentation. In 1982, Fe deposition increased with time throughout the ice-free season, and the rate was higher in Sparkling Lake than the other two lakes. High Fe concentrations in the water column and sediment traps of Sparkling Lake may explain the high C/P ratios in suspended and sinking particulate matter in this lake despite relatively high concentrations of total P (Table 1). The occlusion of a significant portion of the P pool in a colloidal Fe-associated compartment would decrease availability of P to primary producers. Because the major source of sedimenting particles is primary production, the high C/P ratio of particulate matter may result from P depletion through occlusion of P by Fe.

In all three lakes, the C/P ratios of sediment-trap material are much higher than the Redfield ratio of 106 throughout the ice free season (Table 3). The C/N ratios of trap material were also somewhat higher than the Redfield ratio of 6.63 (106:16). Apparently, phytoplankton reach the Redfield C/P ratio only when grown under conditions where P is not limiting growth (Gächter and Bloesch 1985; Goldman et al. 1979). Comparison of C/P to C/N ratios suggests that P generally limits phytoplankton production in these lakes.

By multiplying the concentration of C, N, or P by the mass flux of particles, we can calculate the rate of sedimentation for a given nutrient. With the exception of the trend in C/P discussed above, the nutrient content of trap material remains fairly constant throughout the ice-free season (Poister 1992). Thus, seasonal increases in mass sedimentation (see Fig. 1) correspond to increases in C, N, and P sedimentation. We conclude that the cause of seasonal increases in mass sedimentation, settling of large siliceous algae, also leads to seasonal increases in nutrient removal from the water column to the sediment–water interface.

Water Column Recycling of Nutrient Elements

In lakes, nutrient sedimentation is partially counterbalanced by recycling, whereby biologically occluded forms of nutrient elements are converted to biologically available forms and reused in primary production. To assess recycling, we compare two important fluxes influencing the nutrient status of the photic zone, namely nutrient element sedimentation and fixation. Nutrient fixation represents available nutrient uptake or demand, and sedimentation represents total nutrient removal from the photic zone. We have concluded that material settling from the photic zone of these lakes is mainly algal-

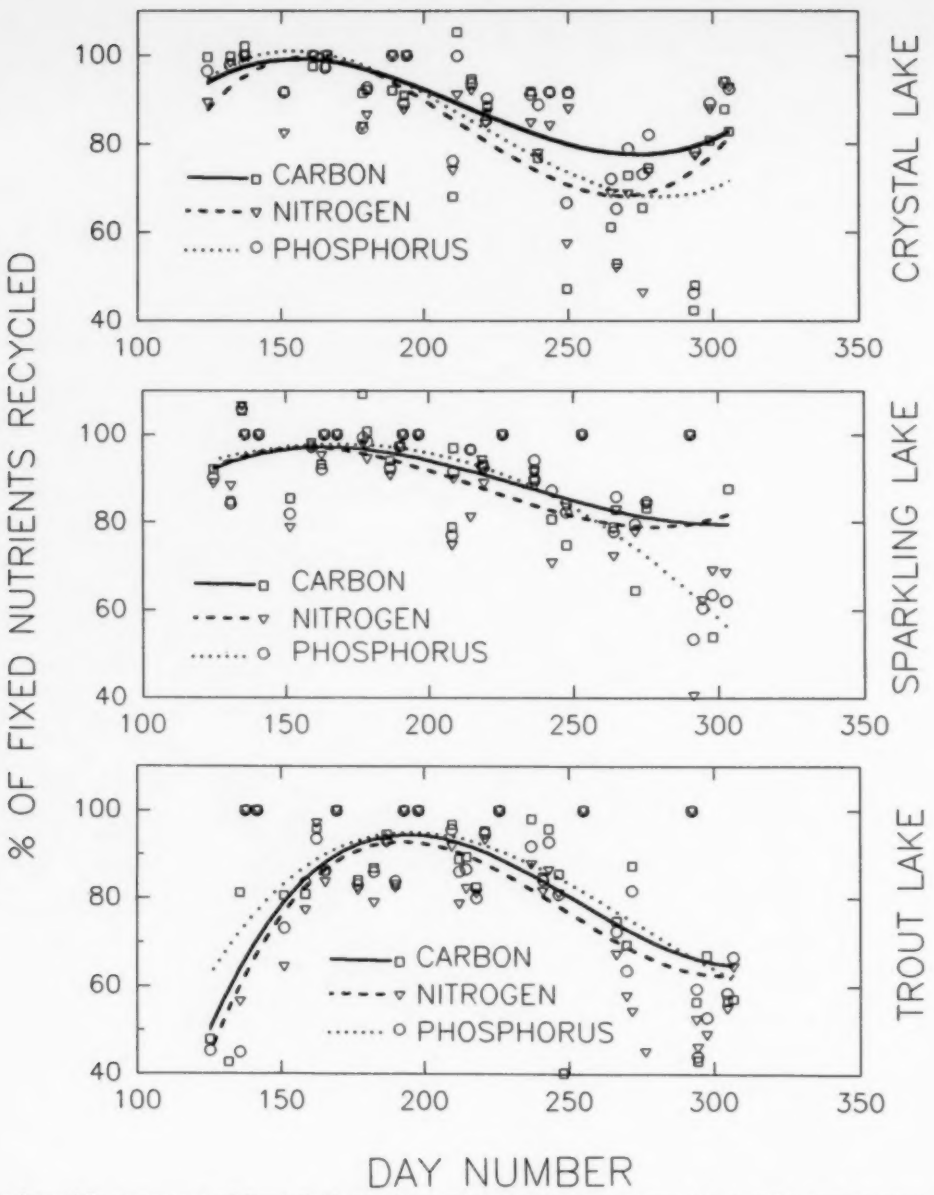

FIG. 4. Seasonal trend in percentage of fixed C, N, and P recycled in the water column ($F_R \times 100$). Best fit lines are shown to clarify trends of the individual nutrients.

derived particulate material. Also, removal of particulate matter by outflow is negligible (Poister 1992). Thus, a nutrient element fixed through photosynthesis can be either sedimented, recycled, or remain in occluded form in the water column. The fraction of the amount of nutrient element fixed through primary production that is recycled in the water column (F_R) can be estimated by the following equation

$$F_R = 1 - \frac{\text{Nutrient sedimentation} \pm \text{changes in standing stock}}{\text{Nutrient fixation during primary production}}.$$

In Crystal, Sparkling, and Trout lakes, the average change in standing stock is about 3% of the average sedimentation rate. Thus, F_R is mainly a function of the ratio of sedimentation to production. The combination of incorporation, change in standing stock, and sedimentation terms in the same units results in a dimensionless recycling term that includes all forms of recycling (cell lysis, zooplankton excretion, microbial degradation, and fish excretion) without accounting for each process individually. We note that our estimate of F_R is conservative owing to sources of nutrient sedimentation other than primary production.

Nutrient-element recycling (F_R) shows both interlake and seasonal trends (Fig. 4). F_R is lower for P than for C or N in

TABLE 4. Nutrient-element recycling in the water column, expressed as a percentage of the amount incorporated during photosynthesis ($F_R \times 100$). Average for ice-free seasons of 1986–91.

	Percent recycled		
	C	N	P
Crystal	88	83	84
Sparkling	88	86	84
Trout	77	74	80

Sparkling Lake in the fall, reflecting the influence of Fe-associated sedimentation of P discussed previously. For all nutrients, F_R during the ice-free season is lower in Trout Lake than in either Crystal Lake or Sparkling Lake (Table 4). The seasonal trends in F_R show that nutrient sedimentation is not a constant proportion of incorporation throughout the ice-free season. Seasonal trends in F_R are the inverse of seasonal trends in mass flux to sediments: large spring and fall sedimentation maxima in Trout Lake and a gradual increase in sedimentation throughout the ice-free season in Crystal and Sparkling lakes (see Fig. 1). Over the ice-free season, 74–88% of the C, N, and P incorporated through primary production is eventually recycled (Table 4), possibly to support more primary production in the water column.

Siliceous algae appear to influence interlake and seasonal trends in recycling, similar to their influence on mass and nutrient sedimentation. The periods of decreased recycling (F_R) correspond to times of dominance of siliceous algae (mostly diatoms) in the phytoplankton community, i.e., the spring and fall diatom blooms. Siliceous algae influence on F_R is most apparent in Trout Lake where siliceous algae make up a larger proportion of the phytoplankton community.

Biomass losses due to sedimentation are greater for diatoms than other phytoplankton (Reynolds et al. 1982; Reynolds and Wiseman 1982). The high sinking rates of diatoms directly influence phytoplankton ecology and periodicity (Reynolds 1973, 1980; Titman and Kilham 1976; Jewson et al. 1981). Furthermore, diatom sedimentation also influences nutrient availability by producing seasonal trends in nutrient recycling. Sholkovitz and Copland (1982) concluded that the nutrient component of sinking diatoms in Windermere was largely recycled in the upper 25 m of the water column. Similarly, Shafer and Armstrong (1994) found substantial recycling of diatom P during sedimentation and burial in the bottom sediments of Lake Michigan. Although recycling of diatom-bound nutrients is substantial in lakes, including the lakes studied here (Poister 1992; Armstrong et al. 1987), sedimentation repartitions nutrients between upper and deeper water, thereby limiting nutrient availability to the photic zone. Thus, sedimentation of siliceous algae influences nutrient availability by reducing recycling within the water column, the major source of nutrient elements to primary producers.

Values of F_R (Table 4) for Crystal, Sparkling, and Trout lakes are consistent with values reported for other lakes. Among several lakes of varying trophic state, average annual sedimentation of C amounted to 14–36% of production (Bloesch and Uehlinger 1990). Our estimates for the ice-free season are 12, 12, and 23% of C production lost to sedimentation or changes in standing stock for Crystal, Sparkling, and Trout lakes, respectively.

Similarly, our estimates of N and P sedimentation and recycling (Table 4) are supported by findings of others that recycling in the water can account for 35–75% of the N and 55–85% of the P needed to maintain primary production throughout the summer (Bloesch et al. 1977). Caraco et al. (1992) found that new production, defined as the production not supported by recycling, accounted for 35% of the total production at midsummer in Mirror Lake. Our results indicate lower proportions of new production, amounting to <25% of total production for the same time period in Crystal, Sparkling, and Trout lakes.

Conclusions

A 6-yr record of sediment trap data from Crystal, Sparkling, and Trout lakes has shown distinct seasonal and interlake trends in nutrient sedimentation that are consistent from year to year. Seasonal increases in mass and nutrient sedimentation are associated with spring and fall blooms of large siliceous algae, mainly diatoms. Thus, we conclude that siliceous algae act as nutrient scavengers by removing nutrients via sedimentation more efficiently than nonsiliceous algae. Sedimentation of Fe-associated P noticeably influences P sedimentation, particularly in Sparkling Lake, where a gradual decrease in C/P molar ratio in sediment-trap material occurs throughout the ice-free season.

Sedimentation is a significant source of nutrient loss from the water column and is the fate of 12–23% of the C fixed through primary production during the ice-free season. Recycling is the largest source of nutrients to primary producers throughout the ice-free season. During the summer stratified period, recycling of P within the water column accounts for 85–90% of P demand from primary production. Thus, lakes receiving little external loading can maintain substantial levels of primary production through internal recycling of N and P.

Through rapid sedimentation, diatoms apparently impede nutrient recycling. Factors favoring production of large siliceous algae should decrease nutrient recycling within the water column. The effect of diatom sedimentation on nutrient availability and the constraints on this mechanism bear further investigation.

Acknowledgements

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Biological Events during Ice Breakup in the Great Whale River (Hudson Bay)

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The physical events and changes of abundance of freshwater and marine organisms were documented daily at the mouth of the Great Whale River to a distance of about 5 km in the freshwater plume extending in Hudson Bay. For the 2-wk period before, during, and after the ice breakup, water flow and concentration of coarse (>500 μm) particulate organic matter (CPOM) decreased, while transparency and temperature increased. The Great Whale River outflow to coastal Hudson Bay for that period was estimated to contain 8.8 t of CPOM and 1021 million insects (primarily simulids). Insect drift was positively related to river flow during daylight hours, whereas night drift intensified with receding flow values. The maximum drift of freshwater–anadromous fish larvae (coregonids and *Lota lota*) coincided with peak flow at ice breakup. A stratified under-ice freshwater plume isolated the freshwater drift material (CPOM, insect larvae, and fish larvae) from the marine community and increased the distance at which terrigenous material was exported into Hudson Bay. During the short period of ice breakup, the Great Whale River contributes substantial amounts of material, which probably stimulates biological production on the coast of Hudson Bay.

Les événements physiques et l'abondance des organismes dulcicoles et marins ont été suivis quotidiennement à l'embouchure de la Grande Rivière de la Baleine jusqu'à une distance de 5 km environ dans le panache d'eau douce qui s'étend dans la baie d'Hudson. Pendant la période de deux semaines qui précède et qui suit le dégagement des glaces, le débit de l'eau et la concentration des grosses particules organiques (>500 μm) ont diminué alors que la transparence et la température de l'eau ont augmenté. Les eaux déversées par la Grande Rivière de la Baleine sur le littoral de la baie d'Hudson pendant cette période renfermaient environ 8,8 t de grosses particules organiques et 1021 millions d'insectes (principalement des simulies). La dérive des insectes était positivement liée au débit de la rivière pendant les heures de clarté alors que la dérive nocturne s'intensifiait avec la diminution du débit. La dérive maximale des larves de poissons dulcicoles et anadromes (corégonidés et *Lota lota*) correspondait au débit de pointe du dégagement des glaces. Un panache d'eau douce stratifié sous la glace isolait la matière dulcicole (grosses particules organiques, insectes et larves de poisson) de la communauté marine et augmentait la distance à laquelle la matière terrigène était transportée vers la baie d'Hudson. Pendant la courte période du dégagement des glaces, la Grande Rivière de la Baleine déverse des quantités substantielles de matière qui stimule probablement la production biologique sur le littoral de la baie d'Hudson.

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A long-standing debate persists on the importance of the outflow of large rivers as a regulating factor for the overall productivity and fisheries recruitment in coastal waters (Sutcliffe 1972; Sinclair et al. 1986; Drinkwater et al. 1991). Although flow alteration through hydroelectric power was hypothesized to exert effects on coastal productivity (Neu 1975), its large-scale cumulative effects in northern waters remain difficult to identify (Bunch and Reeves 1992). Little is known of the processes regulating production in large northern rivers discharging on the Hudson Bay coast, and how river outflow influences production dynamics in northern marine regions (Craig et al. 1984). Anderson and Roff (1980) showed that inshore areas located in the southeastern part of Hudson Bay supported the highest plankton biomass and possibly the greatest productivity. They hypothesized that high phytoplanktonic production might be related to freshwater runoff and mixing regime in that area. The period of ice breakup in the spring coincides with particularly high primary productivity (Legendre et al. 1981). At that time, the seasonal light increase and the low-salinity melting water trigger planktonic growth under the ice surface. In addition, the well-developed epontic flora supports an increased zooplanktonic production (Runge and Ingram 1988). The decay of this flora is shortly followed by ice breakup and the initiation of the phytoplankton bloom (Legendre and Simard 1979).

Regulation of the seasonal flow regime through hydroelectric development in the La Grande River (James Bay) prompted a number of studies on the impacts of its modification (reviewed by Messier et al. 1986). The spring ice breakup is likely a key period of the yearly cycle, because an important part of the yearly discharge and particle export take place during this short period (Likens et al. 1977).

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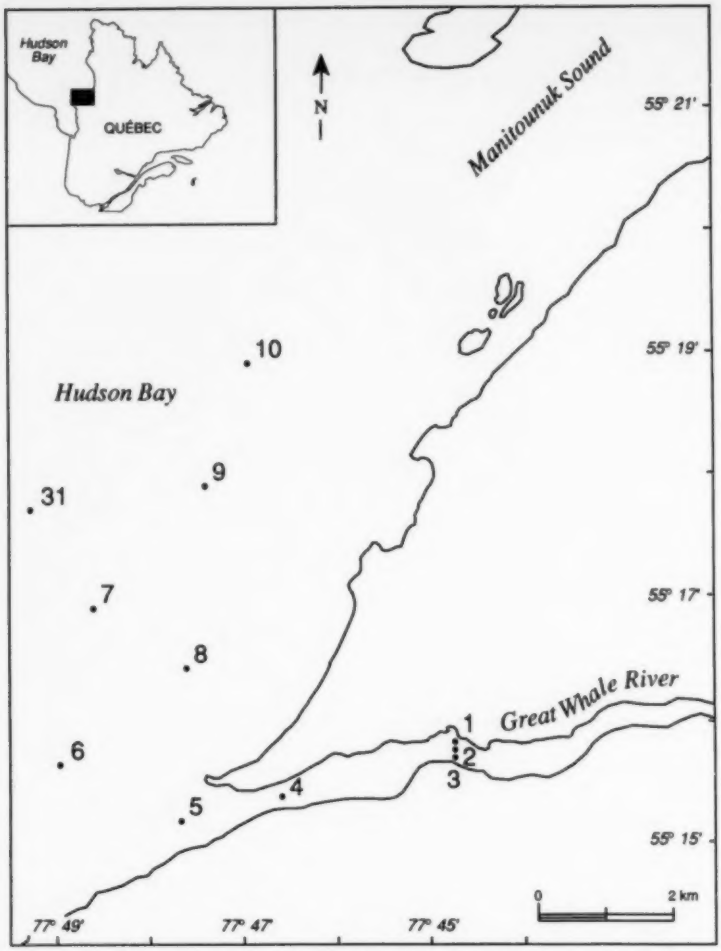

FIG. 1. Location of stations at the mouth and in the coastal plume of the Great Whale River (southeastern Hudson Bay, inset). Stations 5 and 6 mark the edge of the ice pack and open water area on May 23, 1986, which receded to stations 7 and 8 on May 24 and stations 9 and 10 on May 26. Wind pushed the ice back to station 5 on May 28 and to shore (station 4) on May 29. Station 31 is the hydrographic station from Lepage and Ingram (1988).

Furthermore, the remaining winter ice cover on Hudson Bay at the onset of the spring freshet allows the persistence of a freshwater (<5 $mg \cdot L^{-1}$) plume on top of salt water (29 $mg \cdot L^{-1}$) spreading longshore into Manitounuk Sound and as far as 15 km offshore in the bay (Ingram and Larouche 1987), therefore, expanding the area over which freshwater material is exported. These issues are particularly relevant to the Great Whale River, which was, until recently, considered for hydroelectric development.

This study describes the daily physical and biological events occurring in the Great Whale River over a 2-wk period, before, during, and after the ice breakup. The spatial distribution and abundance of organisms through time are described from the mouth of the river to about 5 km in the plume. I evaluated the amount of coarse particulate organic material (CPOM), insects, and fish larvae exported from the freshwater to the marine environment during this period. This information provides insights into the importance of high spring discharge for allochtonous material entering southeastern Hudson Bay.

Study Area

The Great Whale River basin (42 735 km^2) has a mean annual discharge >600 $m^3 \cdot s^{-1}$ and ranks fifth in importance after the LaGrande, Nottaway, Eastmain (before impoundment), and Rupert rivers as a source of fresh water entering eastern Hudson Bay. The Great Whale River is under 1-m-thick ice cover from late November to mid-May. Monthly discharge is lowest during winter (<200 $m^3 \cdot s^{-1}$) and peaks in spring (>1600 $m^3 \cdot s^{-1}$) before decreasing to lower summer levels. Accordingly, about 10% of the yearly discharge takes place during the 2-wk period of spring ice break-up.

The river flows over granitic bedrock of the Canadian Precambrian Shield. The watershed is forested with the boreal assemblage dominated by spruce (*Picea* spp.), tamarack

(*Larix laricina*), and trembling aspen (*Populus tremuloides*) interspersed with areas of lichen and peat bogs. Balsam poplar (*Populus balsamifera*), sweet gale (*Myrica gale*), and speckled alder (*Alnus rugosa*) are found in the riparian areas.

The river drains to southeastern Hudson Bay, which is generally ice covered from December until early June (Larouche and Galbraith 1989). The ice cover in the coastal area of the bay remains intact for 2–3 wk after river breakup, thus providing conditions of high discharge under sea ice cover (Ingram and Larouche 1987). The plume generally extends in a northeasterly direction, producing a slow-moving (0.01 $m \cdot s^{-1}$), permanent brackish (<5 $mg \cdot L^{-1}$) layer under the ice that reaches to Manitounuk Sound, >30 km away (Fig. 1) (Ingram 1981). The surface area of the plume appears correlated to increased river flow, although there is an important year-to-year variability in physical oceanographic conditions (Ingram and Larouche 1987). A review of oceanographic work in southeastern Hudson Bay can be found in Roff and Legendre (1986).

Materials and Methods

Monitoring of Climatological and Physical Conditions

Minimum and maximum daily air temperature were obtained from the Flight Forecast and Weather Service (Environment Canada 1986) for the Great Whale River Airport. Daily flow values ($m^3 \cdot s^{-1}$) for May 1986 and the surface area of the Great Whale River basin were provided by the Service des Relevés aquatiques (Ministère de l'Environnement du Québec 1987).

River water temperature was continuously recorded from May 14 using an thermograph (Ryan Model J) immersed in the intake well of the community water pumping station, located near stations 1–3. Vertical profiles of salinity, temperature, and turbidity were made using a continuous conductivity–temperature–depth (CTD) recorder (Guildline model 8770). Other measurements of surface water temperature were taken with a hand-held mercury thermometer. Water transparency was measured with a 30-cm Secchi disk. Water velocity under the ice and at the surface was measured using a flowmeter (General Oceanics Inc. model 2030).

Biological Sampling

Sampling took place from May 14 to 28, 1986. Prior to ice breakup, sampling was carried out from holes drilled through the ice at the mouth of the river (station 4) and in the plume (station 31) (Fig. 1). As the pack ice started to crack (May 16), additional samples were taken at station 4, from channels of melting water and through crevices wide enough (>50 cm) to insert the net and other apparatus. At ice breakup (May 17), sampling was done from large ice floes stranded along the shore. As soon as the river became navigable (May 19), sampling was carried out daily from a small (5-m) outboard motor boat at three river stations (1–3) located 2.5 km inland. From May 21, night (between 22:00 and 04:00) sampling of stations 1–3 was added to the daytime sampling carried out at the other stations.

As the ice margin receded into Hudson Bay, new stations were progressively added to the daily sampling schedule. At the maximal extension of the lead (26–27 May), 10 stations were sampled, from 2.5 km upriver to about 5 km into Hudson Bay (Fig. 1). On May 28, wind pushed the loose pack ice back to shore, bringing the outer limit of sampling to station 5. The river mouth and bay remained ice jammed for the next 2 wk, preventing further sampling.

Suspended and drifting material was sampled using a 500-μm mesh plankton net mounted on a rectangular (1.0 × 0.5 m) frame, equipped with a flowmeter. The frame could be either suspended from the ice surface with a depressor (in slow-current conditions), held by hand through a hole or crevice in the ice using a 2-m-long aluminum handle screwed to the frame, or towed behind an outboard motor boat for surface (0–1 m) or oblique (0–10 m) tows. This design permitted use of the same net under all sampling conditions, while eliminating the interference of a bridle on water flow. One surface and one oblique tow were made at all stations located in the river plume (stations 5–10) in Hudson Bay.

Samples taken from holes drilled through the ice ($N = 23$), consisted of the material filtered over a 1 to 15-min interval, depending on current speed. Horizontal tows ($N = 78$) from the outboard motor board were standardized to a 15-min duration. For oblique tows ($N = 15$), the net was allowed to sink vertically next to the boat before being pulled back towards the surface at a slow speed. Upon reaching the surface, the net was hauled back to the boat by hand.

Samples were preserved in absolute ethanol or 4% buffered formaldehyde. Each sample was sorted and the organisms were identified and enumerated. The remaining coarse (>500 μm) particulate matter was weighed after drying (24 h at 105°C) and ashing (6 h at 550°C), to calculate ash-free dry weight (AFDW), as an estimator of coarse particulate organic matter (CPOM).

Statistical Analyses

CPOM concentrations and insect abundance at different river sites and at different times of the day were compared using one-way ANOVAs to assess the spatial and temporal variability of drifting material. The following linear regressions were calculated between daily average river measurements of wet, dry, and ash-free dry (AFDW or CPOM) weight:

(1) Dry weight = 0.055 (wet weight) + 2.355,
$r^2 = 0.93$, $p < 0.001$, $N = 13$

(2) AFDW = 0.674 (dry weight) + 0.172,
$r^2 = 0.99$, $p < 0.001$, $N = 13$.

The relationships between daily river flow ($m^3 \cdot s^{-1}$) and CPOM concentration ($mg \cdot m^{-3}$) and insect abundance ($no. \cdot m^{-3}$) during day and night were examined using linear regressions, after log-normal transformation when necessary. Average daily CPOM concentrations (measured) and insect abundance (derived from the regression models) were used to estimate the river export to Hudson Bay during the study period.

Results

Physical Events at Ice Breakup

The spring thaw started inland in the upper basin and gradually proceeded downstream. Average daily air temperatures above freezing were observed from May 7 to 17 (Fig. 2A), and prompted rapid snowmelt, which steadily increased the under-ice flow. Between May 9 and 14, flow at the mouth increased from 350 to 1365 $m^3 \cdot s^{-1}$, and reached

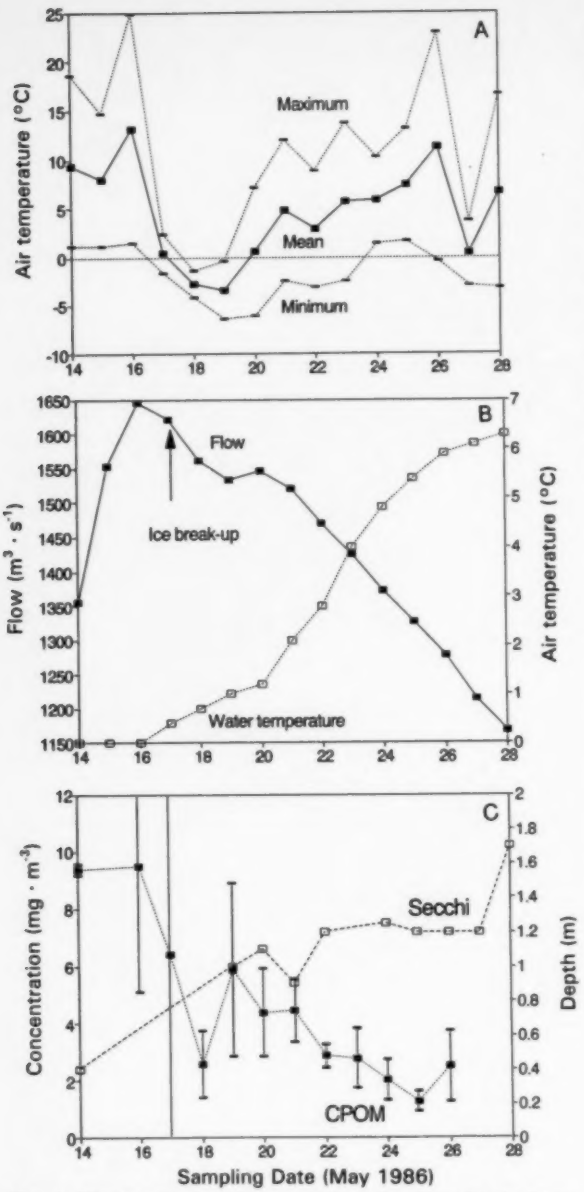

FIG. 2. Physical parameters measured in the Great Whale River during the sampling period. (A) Maximum, mean, and minimum daily air temperature (°C). (B) Daily flow ($m^3 \cdot s^{-1}$, solid squares) and water temperature (°C, open squares) at stations 1–3. (C) Average daily concentration ($mg \cdot m^{-3}$; ±1 SD) of coarse particulate organic matter (CPOM) (solid squares) and Secchi disk transparency (m; open squares) at river stations.

a maximum of 1650 $m^3 \cdot s^{-1}$ 2 d later, at the beginning of sampling (Fig. 2B). Sampling the drift through a hole in the ice (May 14–15) near the mouth of the river proved difficult as current velocity equalled 8–10 $m \cdot s^{-1}$ and the net rapidly (<1 min) filled with frazil and chunks of ice. The water column (7 m) below the ice appeared clogged by frazil, reducing the effective section of the channel. Increased velocities were perceptible by the percussive sounds of ice chunks and vibrations of water flow. The following day (May 16), shallow (<50 cm) channels filled with turbid, slow-moving (<0.2 $m \cdot s^{-1}$) meltwater were formed along the shore. Widening crevices marked the degradation of the ice cover prior to its breakup. The ice had a grayish colour and a wet surface.

Increased flow (Fig. 2B) and exceptionally high (>15°C) daytime air temperatures (Fig. 2A) rapidly weakened the ice. At breakup (May 17), wide crevices and channels of flowing meltwater could be observed along the shore. As the ice started to move very slowly downstream, additional crevices opened in the ice cover and generated floes of various sizes piling up on each other. The initial clearing of the river proceeded in several time intervals (about 15 min) during which slow ice drift alternated with no movement, indicating that ice inertia could only be overcome after a certain water pressure had developed. Ice breakup coincided with peak flow values (Fig. 2B), which remained high for the next 3 d and decreased afterwards. Concurrent drop in river level (>1 m) left large, 1-m-thick ice floes stranded along the shore.

Air temperature dropped sharply to freezing point for the first 3 d of open river water (May 17–19) and subsequently (May 20–28) followed the more usual springtime pattern of daytime thaw (>5°C) and nighttime freeze (<0°C) (Fig. 2A). Accordingly, water temperature rapidly increased as water flow decreased (Fig. 2B). For the 3–4 d after ice breakup, ice floes, tree trunks, and large pieces of wood drifted in the river, making navigation dangerous.

In Hudson Bay, a sharp halocline and turbidity gradient could be observed at 4 m depth below the ice (Fig. 3), confirming the presence of a layer of river water on top of Hudson Bay salt water. Across the pycnocline, water temperature decreased from 0 to −1.5°C, salinity increased from <5 to 27 $mg \cdot L^{-1}$, and light transmission increased from 0–8 to 80%. An identical pattern was found 10 d later at all stations in the plume, indicating that the vertical structure of the weather column had remained stable throughout the sampling period (S. Lepage, Department of Meteorology, McGill University, Montréal, QC, personal communication), owing to the calm weather conditions.

Spatial Homogeneity of Drifting Material within the River

The homogeneity of the sampling sites within the river was verified prior to the description of the temporal changes in the amount of drifting material. This was verified separately for samples collected before and after ice breakup. First, the abundance of organisms collected under the ice was compared (one-way ANOVAs) with that observed in adjacent open water along the river embankment. It was thought that the high turbidity, slightly warmer temperature, and slower velocities provided a potentially more favourable environment for insects and fish larvae found in the channels. No significant differences were found for the mean concentrations of insects or larval fish at each station with respect to ice cover or classes of flow velocity. Abundance of insects (cumulative) ($p = 0.95$, mean = 0.48 individuals $\cdot m^{-3}$) and of burbot (*Lota lota*) larvae ($P = 0.40$, mean = 0.05 individuals $\cdot m^{-3}$) under the ice (16–17 May) did not differ from the nearshore channels.

Second, I compared the concentration of CPOM and insect abundance collected after ice breakup at the three river stations,

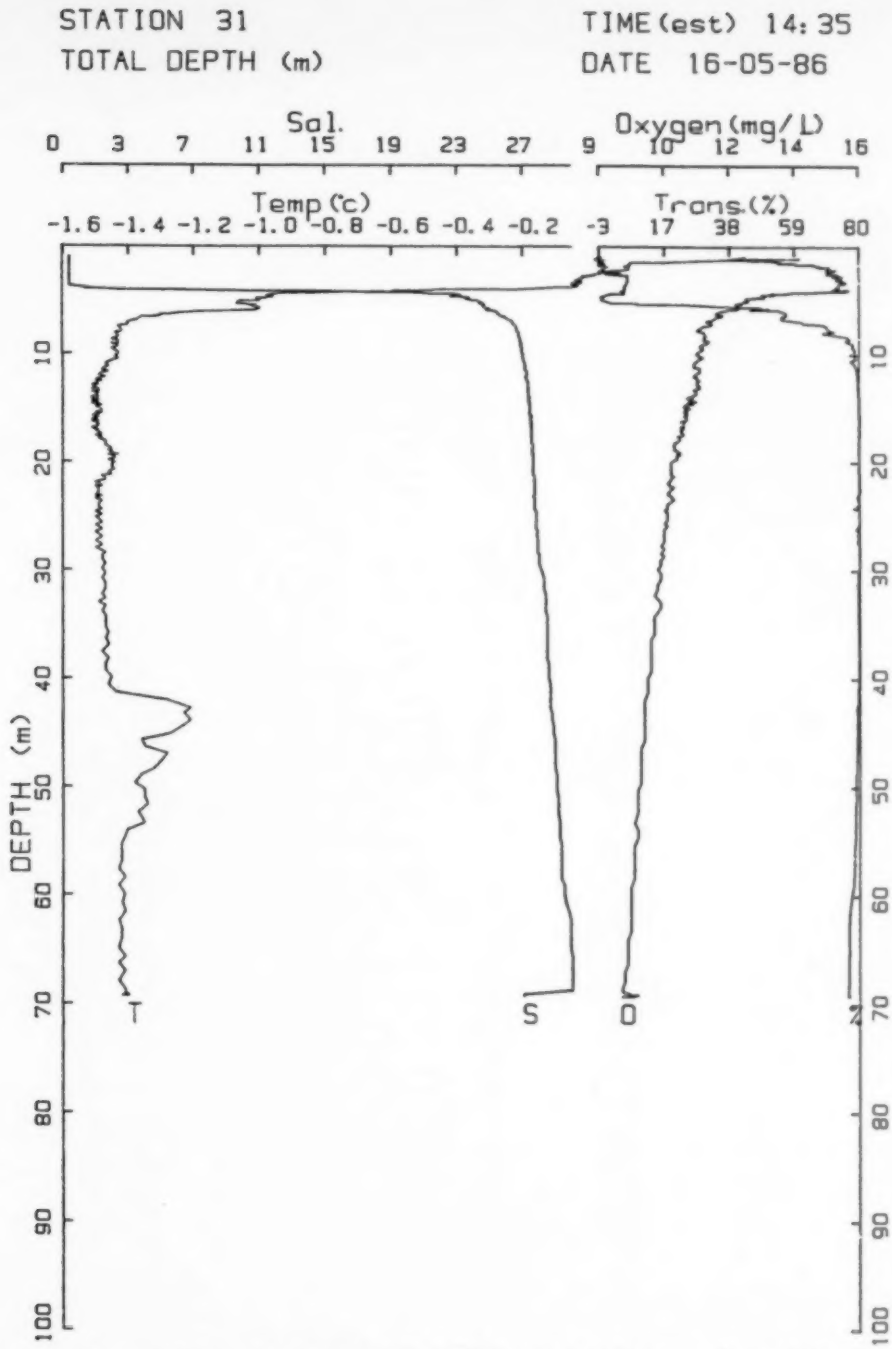

FIG. 3. Vertical profile of temperature (T, °C), salinity (S, $mg \cdot L^{-1}$), dissolved O_2 (O_2, $mg \cdot L^{-1}$), and light transmission (%) with depth (m) in the Great Whale River plume (Station 31, May 16, 1986; from Lepage and Ingram 1988).

located along the north (2–5 $m \cdot s^{-1}$, floodplain, station 1), central (6–10 $m \cdot s^{-1}$, main channel, station 2) and south (11–12 $m \cdot s^{-1}$, floodplain, station 3) parts of the river (Fig. 1), to determine if the distribution of drifting material differed with respect to current velocity and location relative to the main channel. Comparison of the mean concentration of particulate material (by wet, dry, and ash-free dry weight, Table 1) and abundance of the 10 most abundant insect taxa (ANOVA results not shown, see taxa listed in Table 4) showed no difference among sampling locations.

TABLE 1. Comparison of mean concentration ($mg \cdot m^{-3}$) of coarse (>500 μm) particulate organic matter, by wet, dry and ash-free dry weight (AFDW), from collections made in the river main channel (station 2) and in the flooded areas along its sides (stations 1 and 3). The probability associated with the ANOVA F value ($P > F$) is given.

	Station 1 Floodplain	Station 2 Center	Station 3 Floodplain	$P > F$
Wet weight	25.85	52.03	38.53	0.059
Dry weight	4.67	5.87	5.14	0.659
AFDW	2.53	4.29	3.85	0.095
N	11	17	10	

TABLE 2. Comparison of mean concentration ($mg \cdot m^{-3}$) of coarse (>500 μm) particulate organic matter, by wet, dry and ash-free dry weight (AFDW), from collections made at river stations at night (22:00–04:00), morning (04:00–10:00), day (10:00–16:00) and evening (16:00–22:00). The probability associated with the ANOVA F value ($P > F$) is given. *Significantly different ($p < 0.05$).

	Night	Morning	Day	Evening	$P > F$
Wet weight	25.71	53.49	113.71*	43.63	0.026
Dry weight	4.33	6.61	9.37	3.39	0.499
AFDW	2.99	4.83	4.75	3.15	0.151
N	13	2	12	24	

These results indicate that river waters were thoroughly mixed during high springtime flows, and that the organisms were homogeneously distributed across the fast- and slow-flowing areas of the river, thus allowing pooling of the results from all river stations (1–4) to describe temporal changes of drifting material.

Changes of Drifting Material through Time

Coarse particulate material

Coarse particles (>500 μm) consisted mostly of pieces of wood, spruce needles, and fragments of leaves. Concentrations of the CPOM (i.e., AFDW) were high prior to and during ice breakup and decreased in the following days, with a concurrent increase in water transparency (Fig. 2C).

Significant positive relationships were observed between river flow and the log-transformed concentration of the organic (log(AFDW); $r = 0.32$, $N = 61$, $p < 0.05$) and mineral components (log(ash); $r = 0.42$, $N = 61$, $0.01 < p < 0.05$) of coarse (>500 μm) particles. The slightly stronger relationship for log(ash) likely resulted from the accidental retention of sand grains resuspended into the water column at highest velocities, since the mesh size used did not retain silt and clay particles, which constituted the bulk of mineral particles transported by the river.

When samples were compared according to the time of collection, significantly more particles, by wet weight, were found to drift during daytime (10:00–16:00) (Table 2), although no such difference was detected for concentrations of dry and ash-free dry material. This difference could result from methodological error during weighing of wet material, and supported the further use of the less variable CPOM. Estimates of daily CPOM load were obtained from the product of average measured AFDW concentration and flow values, which yielded a value of 8.8 t exported to Hudson Bay between May 14 and 28.

Insects

A large variety of insect larvae, pupae, and adults were collected in the river drift samples (Table 3). Dipterans were by far the most abundant insect order (82% of individuals collected), comprising six families: Ceratopogonidae (one taxon), Empididae (five taxa), Chironomidae (43 taxa), Simuliidae (three taxa), Tabanidae (one taxon), and Tipulidae (three taxa). *Prosimulium* sp. (Simulidae) represented 73% of all insects enumerated and identified. Other groups exhibited a high taxonomical richness in spite of the comparatively small number of individuals collected: Plecoptera (26 taxa belonging to 7 families), Ephemeroptera (21 taxa belonging to 7 families), and Trichoptera (12 taxa belonging to 8 families) represented 11, 6, and 0.6% of all insects collected, respectively. Six species of Plecoptera were captured as emerging adults: *Allocapnia minima*, *Capnia vernalis*, *Paracapnia opis*, *Isoperla marlynia*, *Taeniopteryx nivalis*, and *T. parvula* (Table 3).

Characterization of the habit (mode of existence) and feeding mechanisms (Cummins and Merritt 1984) of the insects collected showed the predominance of clingers (76%) and of filterers, shredders, and collector-gatherers, which represented over 97% of the insects collected (Table 3). This representation was strongly affected by the numerical dominance of *Prosimulium* sp. in most collections.

The 10 most abundant insect species were retained for a more detailed analysis of changes in their daily abundance (Fig. 4). *Capnia vernalis* (Fig. 4A), *Parameletus* sp. (Fig. 4B), and *Tanytarsus–Micropsectra* (Fig. 4C) exhibited a well defined peak of abundance just prior to or concurrent with the ice breakup and decreased afterwards. For *C. vernalis*, this pattern corresponded to its massive emergence as adults. Given the knowledge of the ecology of *Capnia* and *Parameletus* (Olsson and Söderström 1978), it is likely they occupy the upper level of the flooded river bank area, therefore, making them more susceptible to entrainment during the period of highest water levels and erosion by ice. The upper river bank is intensely affected by the erosion produced by the melting snow cover, and susceptible to rapid warming in response to high air temperatures (15–20°C) observed at that time.

Eurylophella minimella (Fig. 4D) exhibited an early peak, followed by a 5-d decrease in abundance before high numbers were observed again. This pattern followed that of air temperature and could be related to its effects on the temporary meltwater streams likely to be used by this species. The low abundances observed between May 18 and 22 followed the decrease of daytime and nighttime air temperatures below the freezing point, and drift resumed as soon as the daily average air temperature rose above freezing. *Ameletus* sp. (Fig. 4E) followed a similar, but less clear, pattern.

Five other taxa, *Prosimulium* sp. (Fig. 4F), *Rheotanytarsus* sp. (Fig. 4G), *Shipsa rotunda* (Fig. 4H), *Podmosta macdunnoughi* (Fig. 4I), and *Eukiefferiella* sp. (Fig. 4J) appeared progressively later and exhibited delayed peaks of abundance through time. This pattern of occurrence in the drift could be related to increased activity levels with water temperature increase, making these species more susceptible to entrainment. This indicates differential physiological responses to the progressive increase in river water temperature.

The occurrence and intensity of night drift in the river was examined on the same group of 10 insect taxa (Table 4).

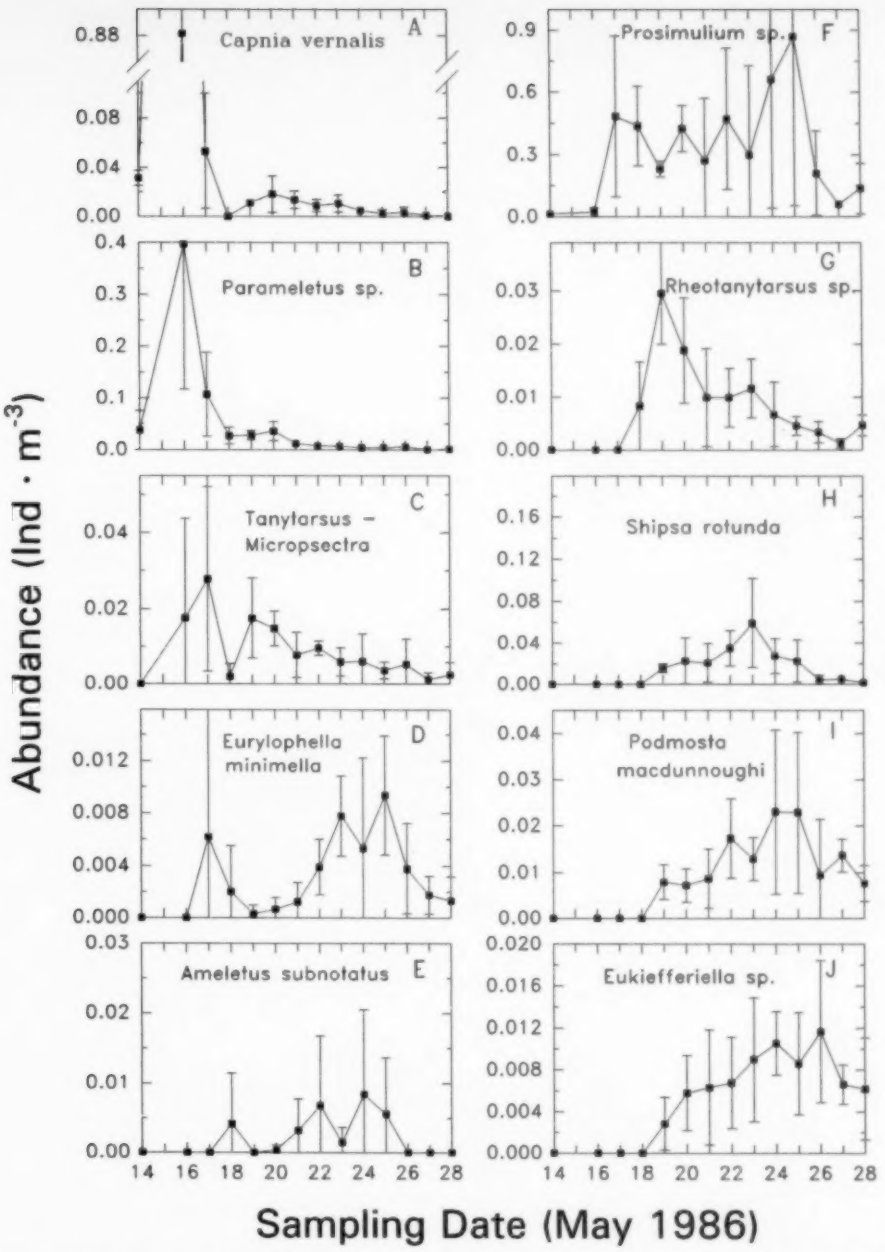

FIG. 4. Average daily abundance (no.·m^{-3}; ±1 SD) of the 10 most numerous insect taxa (panels A–J) at river stations.

Taxon abundance was compared between tows made at night (22:00–04:00), morning (04:00–10:00), day (10:00–16:00), and evening (16:00–22:00). Most insect taxa were significantly more abundant in the night drift (*Eurylophella minimella*, *Prosimulium* sp., *Ameletus subnotatus*, *Shipsa rotunda*, and *Podmosta macdunnoughi*). Two taxa were more abundant in daytime (*Rheotanytarsus* sp. and, marginally, *Tanytarsus–Micropsectra*), whereas the remaining three taxa did not show any significant difference in their daily abundance (Table 4).

The observation of consistent day–night differences in overall insect abundance in the drift prompted the elaboration of two separate models to assess the relationship between river flow and passive (day) or active (night) drift. The linear regressions (Fig. 5) show that flow was positively related to the logarithm of daytime insect abundance ($r = 0.621$, $N = 62$, $p < 0.001$), whereas flow was negatively related to nighttime insect abundance ($r = 0.852$, $N = 12$, $p < 0.001$). Calculation of the expected daily insect drift using these two regressions (Fig. 6) indicated that daytime drift closely

TABLE 3. Abundance (No., number of individuals enumerated) of larval insect taxa in the drift samples of the Great Whale River. Superscript letters next to the number indicate life history stages other than larvae: *a* = emerging adults; i = imago; p = pupae. Mode of existence (ME) and feeding mechanism (FM) correspond to groups defined in Merrit and Cummins (1984). Abbreviations are as follows. Habits: B = burrower; C = clinger; CL = climber; N = net spinner; SP = sprawler; S = swimmer. Feeding mechanisms: C = Collector; F = Filterer; G = Gatherer; P = Predator; PI = Piercer; S = Scraper; SH = Shredder.

Taxon	ME	FM	No.
Arachnida			9
Hydracarina			54
Collembola			27
Plecoptera			
Capniidae	C–SP	SH	2[a]
Allocapnia sp.	C	SH	1
Allocapnia minima (Newport)	C	SH	5[a]
Capnia sp.	C	SH	3
Capnia vernalis Newport	C	SH	390[a]
Paracapnia sp.	C	SH	1
Paracapnia angulata (Hanson)	C	SH	3
Paracapnia opis (Newman)	C	SH	85[a]
Chloroperlidae			
Haploperla brevis (Banks)	C	S	21
Leuctridae			
Leuctra sp.	C–SP	SH	10
Leuctra ferruginea Walker	C–SP	SH	3
Leuctra tenella Provancher	C–SP	SH	16
Leuctra tenuis (Pictet)	C–SP	SH	1
Nemouridae			
Podmosta sp.	C–SP	SH	1
Podmosta macdunnoughi (Ricker)	C–SP	SH	447
Shipsa rotunda (Claassen)	C–SP	SH	780
Pteronarcyidae			
Pteronarcys sp.	C–SP	SH	1
Pteronarcys dorsata (Say)	C–SP	SH	7
Perlodidae			
Cultus decisus (Walker)	C	P	3
Isogenoides frontalis (Newman)	C	P	1
Isoperla sp.	C–SP	P	2
Isoperla bilineata (Say)	C–SP	P	1
Isoperla marlynia Needham and Claassen	C–SP	P	34[a]
Isoperla transmarina (Newman)	C–SP	P	27
Taeniopterygidae			
Taenionema atlanticum Ricker and Ross	C–SP	SH	7
Taeniopteryx nivalis (Fitch)	C–SP	S	6[a]
Taeniopteryx parvula Banks	C–SP	S	1[a]
Ephemeroptera			
Baetidae			8
Baetis sp.	S–C	C–G	69
Baetiscidae			4
Baetisca laurentina Mc Dunnough	C–SP	S–C–G	13
Leptophlebiidae			6
Leptophlebia sp.	S–C	C–G	61
Paraleptophlebia sp.	S–C	C–G	15
Paraleptophlebia cf. adoptiva (Mc Dunnough)	S–C	C–G	1
Siphlonuridae			
Ameletus subnotatus Eaton	S–C	C–G	91
Parameletus sp.	S–C	C–G	426
Ephemerellidae			
Ephemerella sp.	C	S–C–G	10
Eurylophella cf. minimella (Mc Dunnough)	C	C–G	115
Serratella serrata (Morgan)	C	S–C–G	2

TABLE 3. (*Continued*)

Taxon	ME	FM	No.
Heptageniidae			
Heptageniinae	C	S–C–G	6
Epeorus sp.	C	S–C–G	1
Heptagenia sp.	S–C	S–C–G	12
Heptagenia flavescens (Walsh)	S–C	S–C–G	72
Heptagenia cf.pulla (Clemens)	S–C	S–C–G	5
Rhithrogena sp.	C	S–C–G	36
Stenonema sp.	C	S–C–G	2
Ephemeridae			
Litobrancha recurvata (Morgan)	B	C–G	1
Homoptera			19
Heteroptera			1[i]
Corixidae	S	PI	4
Trichoptera			
Brachycentridae			
Brachycentrus sp.	C	F	3
Polycentropodidae			
Neureclipsis sp.	C–N	F	4
Polycentropus sp.	C–N	F	3
Rhyacophilidae			
Rhyacophila sp.	C	P	7
Lepidostomatidae			
Lepidostoma sp.	CL	SH	4
Hydropsychidae			
Arctopsyche sp.	C–N	F	2
Cheumatopsyche sp.	C–N	F	24
Hydropsyche sp.	C–N	F	33
Leptoceridae			
Ceraclea sp.	SP	C–G	2
Mystacides sp.	SP	C–G	1
Hydroptilidae			
Oxyethira sp.	CL	PI	7
Glossosomatidae			
Glossosoma sp.	C	S	1
Hymenoptera			6
Coleoptera			3[a]
Staphylinidae	C–CL	P	4
Elmidae	C–CL	C–G	1
Diptera			
Ceratopogonidae			1
Empididae			
Chelifera sp.	SP–B	P–C–G	10
Clinocera (*Hydrodromia*) sp.	C	P–C–G	2
Dolichocephala sp.	C	P–C–G	1
Hemerodromia sp.	SP–B	P–C–G	1
Wiedemannia sp.	C	P	6
Chironomidae	B	C–G	27[p]
Axarus sp.	SP–B	C–G	22
Cryptochironomus sp.	SP–B	P	13
Cyphomella sp.	B	C–G	23
Dicrotendipes sp.	B	C–E	4
Endochironomus sp.	C	SH	2
Glyptotendipes sp.	B	SH	1
Harnischia sp.	C–CL	S–C–G	2
Microtendipes pedellus De Geer	C–N	F	6
Paracladopelma sp.	SP	C–G	2
Polypedilum sp.	C–CL	SH	25

TABLE 3. (*Concluded*)

Taxon	ME	FM	No.
Robackia sp.	B	C–G	3
Saetheria sp.	B	C–G	4
Stictochironomus sp.	B	C–G	4
Rheotanytarsus sp.	C–N	F	317
Stempellina sp.	SP	C–G	1
Tanytarsus–Micropsectra	C–CL	F	242
Tanypodinae	SP	P	6
Ablabesmyia sp.	SP	P	2
Labrundinia sp.	SP	P	2
Larsia sp.	SP	P	1
Paramerina sp.	SP	P	4
Thienemannimyia sp.	SP	P	88
Zavrelimyia sp.	SP	P	2
Procladius sp.	SP	C–G	21
Diamesinae	C	S–C–G	13
Monodiasema sp.	SP	C–G	8
Protanypus sp.	B	C–G	6
Orthocladiinae	B	S–C–G	50[p,a]
Corynoneura sp.	SP	S–C–G	3
Cricotopus sp.	C	SH	62
Diplocladius sp.	SP	C–G	3
Eukiefferiella sp.	SP	C–G	219
Heterotrissocladius sp.	SP	C–G	87
Limnophyes sp.	SP	C–G	2
Nanocladius sp.	SP	C–G	5
Orthocladius (*Euorthocladius*) sp.	SP	C–G	9
Orthocladius (O.)	SP	C–G	4
Pagastia sp.	SP	C–G	1
Paraphaenocladius sp.	SP	C–G	2
Psectrocladius sp.	SP	C–G	5
Rheocricotopus sp.	SP	C–G	16
Symposiocladius sp.	SP	C–G	1
Tvetenia sp.	SP	C–G	6
Simuliidae			
Cnephia sp.	C	F	46
Ectemnia sp.	C	F	30
Prosimulium sp.	C	F	11 991
Tabanidae			1
Tipulidae			
Dactylolabis sp.	B–C	C–G	1
Dicranota sp.	SP–B	P	22
Gonomyia sp.	B	C–G	1

followed river flow pattern and that nighttime drift became progressively more important as flow receded. Interestingly, the resulting estimate of the number of insects flushed into Hudson Bay remained roughly around 65 million per day, although the relative contribution of day and night drift changed considerably during the 2-wk sampling interval (Fig. 6). An estimated 1021 million insects were carried into Hudson Bay during the study period.

Ichthyoplankton

Two taxa of freshwater–anadromous ichthyoplankton were captured in the river drift. Burbot (*Lota lota*) larvae comprised the bulk (94% of fish larvae in the river), whereas coregonid larvae (6%) were occasionally captured. Burbot larvae were captured in 25% of river tows, with a maximum concentration of 0.06 individuals·m^{-3} in a single tow. Mean daily abundance peaked on the day after ice breakup and progressively decreased later, allowing an estimate of roughly 5 million burbot larvae drifting into Hudson Bay during the study period. Highest abundance of coregonid larvae (0.03 individuals·m^{-3}) was observed under the ice on May 14. Coregonid larvae were captured sporadically (5% of river tows) and in very low numbers (<0.002 individuals·m^{-3}), thus preventing an estimation of their number carried into the bay. Neither taxon was captured in sufficient abundance to test differences of abundance with station or time of the day.

Sampling off Coastal Hudson Bay

A variety of marine invertebrates was captured in the oblique tows made in coastal Hudson Bay (stations 5–10; Fig. 1), indicating they were restricted to the marine waters

TABLE 4. Comparison of mean abundance (individuals·1000 m^{-3}) of the 10 most abundant insect taxa collected at stations 1–3 in the Great Whale River. Values followed by different letters are significantly different from each other. The probability of the ANOVA F value ($P > F$) is given.

Insect taxa	Night	Morning	Day	Evening	$P > F$
Capnia vernalis	7.4a	11.2a	11.3a	7.0a	0.649
Parameletus sp.	7.4a	6.5a	18.3a	11.7a	0.272
Tanytarsus–Micropsectra	7.6a	15.8a	13.7a	5.7a	0.055
Eurylophella minimella	7.4a	1.9b	1.9b	2.8b	0.004
Prosimulium sp.	995.0	234.6b	243.0b	163.5b	0.001
Ameletus subnotatus	11.6a	0.0b	0.3b	0.1b	0.001
Rheotanytarsus sp.	8.4b	18.6a	20.3a	7.3b	0.002
Shipsa rotunda	37.4a	0.0b	28.7ab	14.6ab	0.042
Podmosta macdunnoughi	25.0a	9.3b	10.7b	8.3b	0.001
Eukieffierella sp.	8.7a	8.4a	4.4a	7.2a	0.208
N	13	2	12	25	

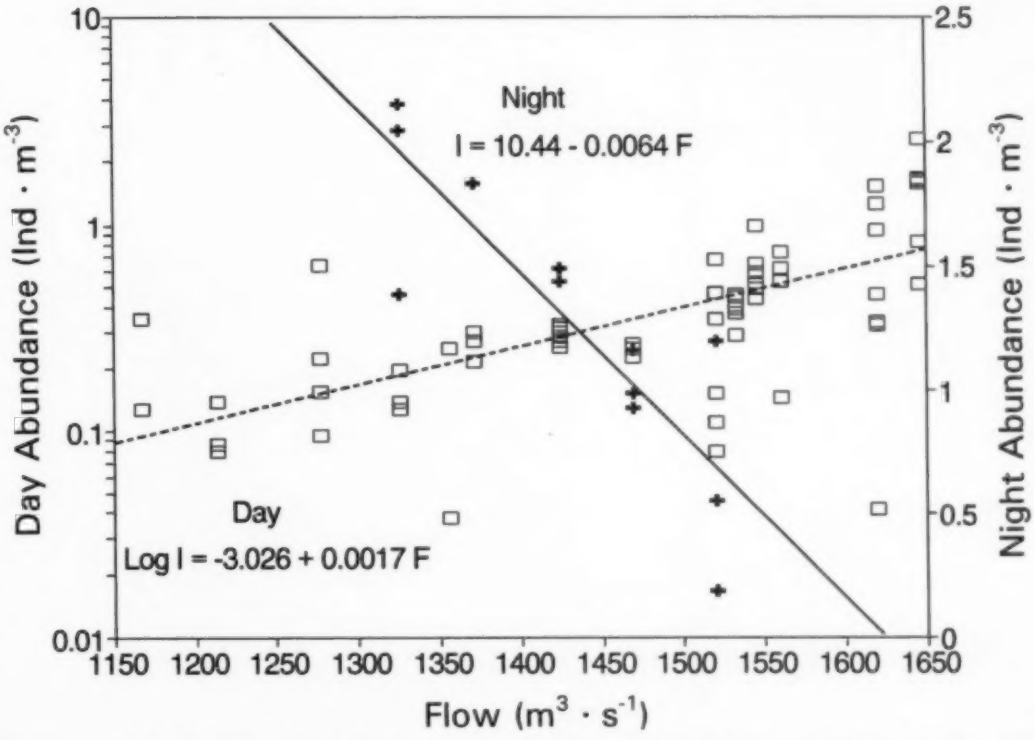

FIG. 5. Linear regression models between day (left Y-axis, open squares) and night (right Y-axis, crosses) insect abundance (I, no.·m^{-3}) and river flow (F, $m^3 \cdot s^{-1}$). Regression equations for the day and night values are indicated; additional information on the regression models is given in the text.

directly beneath the plume: chaetognaths (*Sagitta elegans* and *S. maxima*), euphausiid and decapod larvae, cnidarians (*Aglantha digitale*), and pteropods (*Spiratella helicina*) were the most abundant organisms. Chaetognaths were by far the most abundant group, reaching abundances up to 8 individuals·m^{-3}. The stations most distant from the river mouth (stations 9–10) appeared somewhat richer in marine organisms, although no obvious pattern of abundance or distribution could be discerned otherwise.

Larvae of marine fish species were also collected in oblique tows: *Boreogadus saida* (up to 0.30 individuals·m^{-3}) and *Ammodytes* spp. (up to 0.26 individuals·m^{-3}) were the most abundant, although *Mallotus villosus* and unidentified gadid (possibly *Gadus ogac*), stichaeid, and cottid larvae were reported in small numbers. Adult sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) were captured at all Hudson Bay stations, in surface as well as oblique tows, indicating their presence in the plume as well as underneath it.

The delayed sedimentation of the freshwater material found in the plume was reflected by the presence of a high turbidity layer (<10% transmission) at the pycnocline (Fig. 3). Drift material originating from the river was found in all

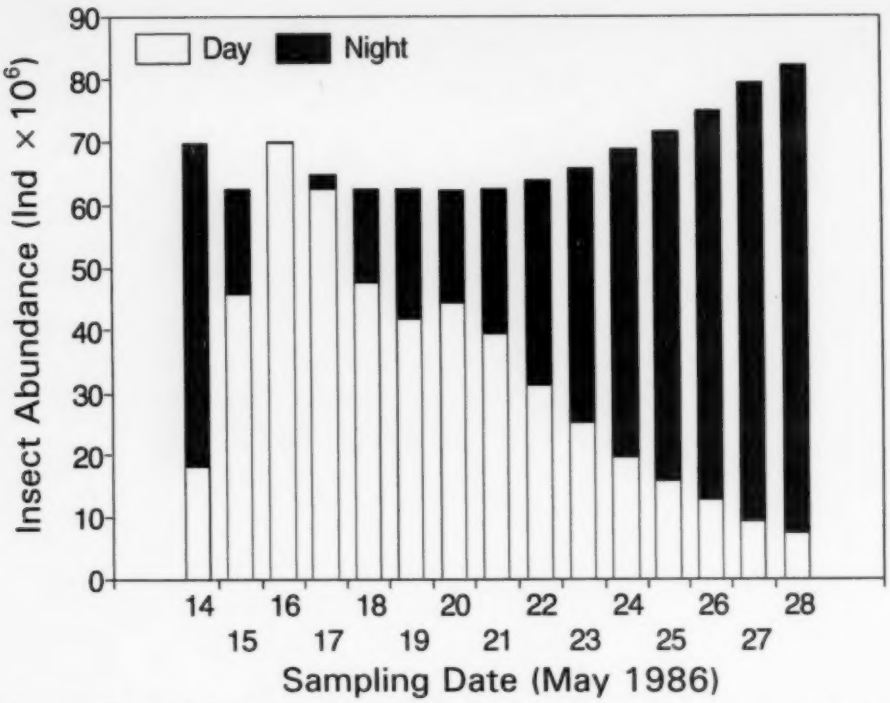

FIG. 6. Number of insects drifting daily from the river into Hudson Bay, predicted from the regression models in Fig. 5. The contribution of day (open bar) and night (solid bar) drift to total daily number is specified.

horizontal tows conducted in Hudson Bay, in decreasing abundance with distance from river mouth. For example, on a complete series of stations samples on May 26, CPOM concentration in the river equalled 2.51 ± 1.45 mg·m^{-3} (mean ± SD; $N = 4$), decreasing to 0.61 and <0.1 mg·m^{-3} at stations 5 and 6–8, located 1 and >3 km from the mouth, respectively. Over the 3-d period over which stations 1–10 could be sampled (May 25–27), average insect abundance decreased from 0.45 ± 0.43 individuals·m^{-3} ($N = 10$) at river stations 1–4, to 0.17 ± 0.25 individuals·m^{-3} ($N = 3$) at station 5 (1 km outside) and < 0.05 individuals·m^{-3} at stations 6–10. Burbot (0.001–0.1 individuals·m^{-3}) and coregonid (0.002–0.03 individuals·m^{-3}) larvae were found as far as stations 9 and 6, respectively. The small number of samples, low abundance, and large variability of measurement precluded any further calculations using freshwater plume organisms.

Discussion

The sequence of events occurring at ice breakup have rarely been described with respect to the relationships between physical and biological processes. This study provides some insights about this complex series of events and assesses some of the contributions made by the Great Whale River to the coastal ecosystem of Hudson Bay.

From the hydrological standpoint, the ice breakup is a dramatic event: the greatly increased water level in the lower reaches detaches the ice cover from the sides of the channel, breaks it in large slabs, and produces ice jams that further increase water level; large plates of ice are carried downstream and many are left stranded on the shores when the water recedes (Mackay and Loken 1974). The high discharge together with the erosion of the embankment caused by the spring ice run and meltwater (Bird 1974) contribute to water turbidity and the flushing of particles into the river. The entrainment of particles and insects in the river is further enhanced by the thawing and subsequent flooding of the riparian area, previously exposed and frozen during the winter.

However, in spite of their high visibility in river waters, coarse particles represent only a minute fraction of the total suspended load in the Great Whale River. Additional seston measurements in the Great Whale River during 1990–91 (C. Hudon, unpublished data), indicate that the entire organic component, of which the coarse fraction (CPOM >500 μm) represents about 0.1%, accounts for about 10% of all (mineral and organic) suspended matter (>0.45 μm) in the river. The yearly particulate load (>0.45 μm) of the Great Whale River was previously estimated at 5×10^5 t (d'Anglejan and Biksham 1988). The additional (yet unmeasured) contribution of dissolved matter brings the present estimate of 8.8 t CPOM released over 15 d to a tiny portion of total river exports.

Terrestrial organic material resuspended in the river is initially subjected to a physical degradation through leaching of soluble compounds and mechanical breakup (Petersen and Cummins 1974), following a number of modifications through which it enters the food chain. The organic material is initially colonized by bacteria, fungi, and microalgae, which accelerate the decomposition and increase its palatability for aquatic insects. At this stage, shredding and rasping insects take an important part in the breakdown process of

the organic litter (Richard and Moreau 1982). Their role is particularly important in the oligotrophic, acidic waters of northern ecosystems, where bacterial contribution is reduced (Hynes et al. 1974). In this study, it is notable that most insects collected in the drift belonged to feeding groups associated with the processing of organic particles of different size fractions. Shredders are responsible for the initial breakdown of CPOM into FPOM (fine particulate organic matter), which is then readily used by filterers and collector–gatherers (Cummins and Merritt 1984). Richard and Moreau (1982) showed that the joint action of insects and microorganisms resulted in a loss of 60–90% of the initial weight of submerged leaf litter after 73 d incubation during summer in a northern stream.

Insect populations of large northern rivers are poorly known, especially for larval stages occurring at the time of ice breakup; the early instars of several species collected in this study were kept as voucher specimens (L. Cloutier, Département des Sciences Biologiques, Université de Montréal, Montréal, QC, personal communication). Large rivers have seemingly few invertebrates and the benthos is dominated by Chironomidae, Ceratopogonidae, and Oligochaeta; Ephemeroptera, Trichoptera, Nematoda, Crustacea, and Mollusca are sometimes mentioned. Higher populations occur in the slow lateral reaches, particularly in the standing waters of the floodplain; the central channel may only contain small psammophilic species of Chironomidae, Oligochaeta, and Nematoda (see reviews by Harper 1981; Barton 1986).

This study confirmed that the life history of certain insect and fish species is finely tuned to the events of ice breakup and spring freshet. At northern latitudes, insects were reported to be more opportunist, flying and mating as soon as conditions are adequate (Downes 1965; Barton 1986). The dramatic emergence of *Capnia vernalis* with the increase in daytime temperatures (May 16, Fig. 4A) represents a classic example of the short-term opportunistic response to environmental conditions. Species inhabiting large rivers and emerging early must take advantage of the ice breakup because it is their only opportunity to avoid being flushed out to sea. Other species' abundance responded to short-term fluctuations of air temperature (*Eurylophella minimella* and *Ameletus subnotatus*; Fig. 4D and 4E) and to rising water temperature (*Prosimulium* sp., *Podmosta macdunnoughi*, and *Eukiefferiella* sp.; Fig. 4F, 4I, and 4J).

During winter, drift densities are minimal, but benthic densities peak owing to deep-water aggregations of animals avoiding the frozen areas of the stream bed (Clifford 1978). Chironomidae contributed 76.2% of the winter benthic standing stock in the Mackenzie delta (Barton 1986). Many first-order streams freeze to the bottom and activity ceases completely until spring (Barton and Wallace 1980). Drift patterns have been extensively studied, and animals classified as day-active or night-active (Harper 1981). These patterns correspond to those observed in our study, which showed the temporary alteration of the drift pattern over the period of high flow and ice breakup. During daylight hours, insect drift appeared to be determined primarily by flow conditions, whereas active night drift was progressively reinstated as flow receded (Fig. 5). The relative importance of night and day drift thus varied rapidly during the period of study, although the resulting daily insect load was relatively stable through time (Fig. 6). This observation points out the importance of estimating insect activity and concentration throughout the daily cycle to assess accurately their abundance. Insect drift to the coastal environment over the course of the study was substantial (1021×10^6 individuals), and readily explains the previously reported congregation of fish in James Bay estuaries at this time of the year (Morin et al. 1992).

Once the particles and insects became part of the drifting material, the downstream movements appeared to be passive and no differential sedimentation or behaviour could be observed (Tables 1–2). This was shown by the lack of significant difference in CPOM concentration and insect abundance at different river stations, and indicated that repetitive sampling at a single, central river station provided a representative estimate of drifting material.

In the Great Whale River, the peak of occurrence of coregonid and burbot larvae occurred on the day of the ice break-up and these larvae disappeared within the following 2 d. Larval coregonids (*Coregonus albula* and *C. lavaretus*) in Norwegian rivers drift downstream from the onset of the yearly spring runoff, for up to 2–5 wk (Naesje et al. 1986). As with our study, the peak of drift occurred during the period of high water discharge, but did not correspond with the increase in water temperature reported for the Norwegian study. It is possible that the short duration of the coregonid drift observed in the Great Whale River is due to the small size of the adult population (R. Morin, Department of Fisheries and Oceans, Moncton, NB, personal communication).

In a well-mixed estuary, allochtonous particles and colloidal material from freshwaters coagulate as they come in contact with the salt water, owing to the decrease in their surface charges towards zero (Knox 1986). Consequently, all of the particulate matter settles in the estuary. However, in a stratified system such as that of the Great Whale River plume, the persistence of the freshwater layer under the ice of Hudson Bay considerably increases the surface area over which allochtonous material settles. The delayed sedimentation is reflected by the important turbidity gradient observed at the interface between the plume and the underlaying salt water (Fig. 3).

As expected, marine zooplankters were found only in oblique tows, which sampled the marine waters lying below the freshwater plume. The zooplankters found in this study are commonly found in marine coastal waters of eastern Hudson Bay (Rochet and Grainger 1988). Chaetognaths (Thuesen and Bieri 1987), cnidarians, and ctenophores (Purcell 1985) are known predators of fish larvae, but these exclusively marine species cannot prey on the fish and insect larvae occurring in the freshwater plume lying directly above, as long as stratified conditions prevail. Of the potential predators observed in Hudson Bay, sticklebacks could be favored by their wide salinity tolerance to utilize both water layers equally well.

Although dissolved material was not measured in this study, the river also exports nutrients (especially nitrogen) and organic carbon (DOC); these were reported to limit production of phytoplankton (Legendre and Simard 1979), ice algae (Demers et al. 1989), and aquatic bacteria (Bunch and Harland 1990) in arctic marine coastal waters. In conjunction with the outflow of particulate material, insect larvae, and fish larvae, the overall imports to the coastal waters from the river appear substantial and could contribute significantly

to the overall coastal water productivity of Hudson Bay (Anderson and Roff 1980).

Benthic productivity should be enhanced by the inflow of particulate organic carbon, particularly in the shallow areas supporting eelgrass beds, which represent an important habitat (Dignard et al. 1991) and support an elaborate food web for invertebrates, fish, and waterfowl (Craig et al. 1984). Previous studies of the macrobenthic community carried out in the Eastmain River estuary (James Bay) prior to flow reduction showed the predominance of chironomids in the fresh waters, while the mollusc *Macoma balthica*, and two species of deposit-feeding polychaetes (*Terebellides stroemi* and *Aglaophamus neotenus*) dominated the estuarine area (Grenon 1982). It is noteworthy that all of these species are users of particulate organic carbon, either in suspension as filter feeders (chironomids: Merritt and Wallace 1981) or in the sediment as selective deposit feeders (polychaetes: Grenon 1982; *Macoma balthica*: Brafield and Newell 1961). These species are likely to be the initial links of carbon transfer from allochtonous origin to the marine food chain in James Bay and Hudson Bay.

Further studies are needed to determine the extent to which the Great Whale River contributes to biological production of coastal southeastern Hudson Bay (Bunch and Reeves 1992). In a shallow coastal lagoon in Beaufort Sea, carbon from terrigenous peat only accounted for 10% of the total organic carbon produced (Craig et al. 1984). Seasonal measurements of the outflow of nutrients, particulate material, and DOC are required to evaluate the year-round contribution of the Great Whale River to coastal Hudson Bay. In this context, a central question concerning the functioning of this ecosystem is whether the organic matter is processed in situ or whether a major proportion is exported towards adjacent waters (Knox 1986). The present study suggests that large quantities of organic and biological particles are exported to coastal waters during spring ice breakup, thus contributing to the overall production of coastal southeastern Hudson Bay.

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Role of the Gills and Gill Chloride Cells in Metal Uptake in the Freshwater-Adapted Rainbow Trout, *Oncorhynchus mykiss*

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Zia, S., and D.G. McDonald. 1994. Role of the gills and gill chloride cells in metal uptake in the freshwater-adapted rainbow trout, *Oncorhynchus mykiss*. Can. J. Fish. Aquati. Sci. 51: 2482–2492.

Fish gills are a primary target of metals from the external environment and serve as a major route for metal uptake. After 12-h exposures to 1 μM ^{109}Cd, ^{65}Zn, or ^{64}Cu in "Ca^{2+}-free" water, gills concentrated metals 3 to 11-fold and contained 38–50% of the total metal burden while sustaining only minor epithelial damage. A twofold increase in chloride cell (CC) surface area had no effect on Cu uptake and actually decreased Zn uptake, confirming that CCs are not primarily involved in the uptake of either metal. In contrast, Cd uptake increased with CC proliferation. Autoradiography revealed a high degree of localization of ^{45}Ca in chloride cells confirming their primary role in Ca^{2+} uptake, whereas Cd and Zn were uniformly distributed amongst all gill epithelial cells. Because CCs did not specifically accumulate ^{109}Cd, we propose that other effects of softwater acclimation were responsible for the increased uptake of Cd. The only cells in the gills specifically accumulating Cd and Zn were eosinophilic granulocytes localized in the central sinus of gill filaments. Autoradiography of liver and kidney tissue showed uniform distribution of ^{109}Cd and ^{65}Zn, i.e., there were no cells specifically accumulating metals in these tissues.

Les branchies des poissons sont une cible importante pour les métaux présents dans l'environnement et elles constituent une des principales voies de captation des métaux. Après des expositions de 12 h à des concentrations de 1 μM de ^{109}Cd, de ^{65}Zn ou de ^{64}Cu dans une eau exempte de Ca^{2+}, les branchies avaient concentré les métaux de 3 à 11 fois et renfermaient de 38 à 50% de la charge métallique totale tout en ne montrant que des lésions épithéliales mineures. Un doublement de la surface des cellules à chlorures n'a eu aucun effet sur la captation du Cu mais a réduit la captation du Zn, ce qui confirme que la captation de ces deux métaux ne constitue pas le rôle premier de ces cellules. Par contre, la captation du Cd a augmenté avec la prolifération des cellules à chlorures. L'autoradiographie a révélé un degré élevé de concentration de ^{45}Ca dans les cellules à chlorures, ce qui confirme leur premier rôle dans la captation du Ca^{2+}; le Cd et le Zn étaient distribués uniformément parmi toutes les cellules épithéliales des branchies. Comme les cellules à chlorures n'ont pas accumulé le ^{109}Cd de manière spécifique, nous croyons que d'autres effets de l'acclimatation à l'eau douce sont à l'origine de la captation accrue de Cd. Les seules cellules des branchies qui ont accumulé le Cd et le Zn de manière spécifique sont les granulocytes éosinophiles situés dans le sinus central des filaments des branchies. L'autoradiographie des tissus hépatiques et rénaux a montré une distribution uniforme de ^{109}Cd et de ^{65}Zn, ce qui signifie qu'aucune cellule n'a accumulé les métaux de manière spécifique dans ces tissus.

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There is now a large body of specific evidence that the gills are the primary site of metal uptake from the environment in fish (e.g., Mn and Zn, Pentreath 1973, 1976; Zn, Spry and Wood 1988; Cd, Williams and Giesy 1978; Pärt et al. 1985; Hg, Olson et al. 1978; Ni, Tjälve et al. 1988). However, the exact route(s) by which metals pass through the gills are not known. Any of the three main cell types found in the gills i.e., pavement cells, mucous cells, and chloride cells (cf. Laurent 1984), could be involved but attention has focused largely on the chloride cells (CCs) because of their putative role in ion transport even though they occupy only about 7% of the total surface area (Potts 1977). Although, in fact, no study to date has proven conclusively that CCs are the gill ion transport cells, there is strong circumstantial evidence favoring this interpretation: they have a higher metabolic rate than other epithelial cells (Perry and Walsh 1989), their morphological appearance is that of transport cells (high mitochondrial density, rich in tubular endoplasmic reticulum; Laurent 1984), and they proliferate in response to ion depletion resulting from exposure to ion-poor media (low Na^+, Laurent and Dunnel 1980; Laurent et al. 1985; Avella et al. 1987; low Ca^{2+}, Perry and Wood 1985). Indeed, there is a significant positive correlation between fractional CC surface area and ionic influx (Na^+, Perry and Laurent 1989; Perry et al. 1992; Ca^{2+}, Perry and Wood 1985). Finally, specific ultrastructural evidence for Ca^{2+} transport by CCs has been provided by Ishihara and Mugiya (1987) who localized oxalate-precipitated Ca^{2+} within chloride cells using transmission electron microscopy.

It is this putative capacity of CCs to transport Ca^{2+}, in particular, that has led to the notion that these cells are responsible for metal uptake. Spry and Wood (1988), for example, showed that CC proliferation in rainbow trout

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(*Oncorhynchus mykiss*), induced by softwater acclimation, was accompanied by an increased Zn influx in the perfused head preparation, suggesting that Zn follows the Ca^{2+} pathway for uptake. Furthermore, there is now strong evidence for a competitive antagonism between metal uptake and Ca^{2+} uptake. Cd and Zn both inhibit Ca^{2+} uptake (Cd, Verbost et al. 1987, 1989b; Reid and McDonald 1988; Zn, Spry and Wood 1989) while increasing Ca^{2+} in the water has been shown to inhibit Cd and Zn uptake (Cd, McDonald et al. 1989; Wicklund 1990; Zn, Spry and Wood 1989). These studies suggest that Ca^{2+}, Cd, and Zn may share the same channel for entry into epithelial cells, which, under normal circumstances, is used for Ca^{2+} absorption.

Therefore, the main objective of this study was to seek specific proof for chloride cells as a route for metal uptake across the gills. For this we employed a stepwise approach, starting with the characterization of uptake of radiolabelled metals (^{109}Cd, ^{65}Zn, and ^{64}Cu) by the gills and subsequent distribution to blood and key target tissues (liver and kidney) over a 12 to 24-h period. Comparisons amongst metals were facilitated by using each at the same low concentration (1 μM) in a simplified water chemistry (circumneutral pH, very low Ca^{2+}). Secondly, we examined whether metal uptake could be stimulated by inducing CC proliferation in the gills (through exposure to low-ion water for 2 wk prior to metal exposure). Thirdly, we developed a new technique for the in situ localization of metals using autoradiography in an attempt to identify specific routes of movements of metals (Cd and Zn only, Cu is unsuitable because of its short half-life) through the gills. As a specific test for this procedure, we also examined the distribution of ^{45}Ca in gill cells, because CCs are known to accumulate Ca^{2+} (Ishihara and Mugiya 1987). Finally, we report on the potential of our autoradiographic technique for the evaluation of impact of metals on other tissues (liver and kidney).

Although metal autoradiography has previously been used in fish to examine tissue distribution of Cd (Tjälve and Gottofrey 1986) and Ni (Tjälve et al. 1988) the whole-body imaging technique employed in these studies does not permit the localization of metals to specific cells. Improving resolution requires light-microscopy autoradiography on thin sections. However, one needs then to be concerned that substantial losses of metals may occur when conventional techniques for the preparation of thin sections are employed. One solution is to employ cryotechniques to retain metals within tissue sections (Morgan 1985), but these techniques typically result in poor-quality sections. Our approach was instead to use conventional light-microscopy section techniques but to minimize metal losses by histochemically precipitating the radiolabel using either Na_2S for metals (Danscher 1981) or the pyro-antimonate method for Ca^{2+} (Van Iren et al. 1979).

Materials and methods

Experimental Animals

Juvenile rainbow trout (12–27 g) were obtained from Rainbow Springs Hatchery, Thamesford, Ont., and held in large polyethylene tanks supplied with well-aerated, dechlorinated municipal tap water at 11–15°C. This water contains about 1 $mmol \cdot L^{-1}$ Ca^{2+} and 0.6 $mmol \cdot L^{-1}$ Na^+ and, hence, is regarded as hard water (Alabaster and Lloyd 1980). Trout were fed three times per week with commercial trout pellets while in the holding facilities. For trout studied in hard water, acclimation to temperature of 12–13°C was commenced 9–12 d prior to experimentation. Feeding was stopped 4–5 d prior to experimentation.

Experimental Series

Softwater acclimation

Softwater acclimation was accomplished by holding trout in a 350 L, temperature-controlled tank (12–13°C) for 2–4 wk. Soft water was prepared by diluting dechlorinated tap water with deionized water and adding NaCl to get the desired composition (Ca^{2+} = 50 $\mu mol \cdot L^{-1}$, NaCl = 70 $\mu mol \cdot L^{-1}$). The acclimation medium was changed every 3 d to maintain ionic composition and reduce buildup of waste products. Fish were fed three times per week during acclimation.

Metal uptake in hardwater- and softwater-acclimated fish

Metal uptake by hard- and soft-water acclimated fish was studied by exposing fish to radioactive metal solutions. Fish were statically exposed to 1 $\mu mol \cdot L^{-1}$ concentrations of Cd (as $CdCl_2$), Cu (as $CuCl_2$), or Zn (as $ZnCl_2$) for up to 24 h. Water pH for all exposures averaged 6.7 ± 0.2. The radioisotopes of Cd and Zn (^{109}Cd, ^{65}Zn) were purchased from New England Nuclear (NEN), while Cu (^{64}Cu, $t_{1/2}$ = 12.9 h) was produced by neutron activation in the McMaster University Nuclear Reactor. Analytical grade salts of Cd, Cu, or Zn (BDH chemicals) were added to the radioisotope solutions to give a final specific activity of 0.19 $MBq \cdot \mu mol^{-1}$. The metal-exposure medium was prepared by using an artificial Ca^{2+}-free water (Ca^{2+} ~ 0.4 $\mu mol \cdot L^{-1}$) to minimize interactions between metal ions and other divalent ions present in the test medium. NaCl was adjusted to normal tap water levels (~0.5 $mmol \cdot L^{-1}$). Exposures were conducted in 2 L of test medium in rectangular containers (total volume = 3.8 L, dimensions = 15.5 cm H × 10.5 cm W × 10.5 cm L, fabricated from black plastic sheet and heat sealed to final shape) fitted with air lines for mixing and aeration of the medium and immersed in a temperature-controlled water bath. A separate container was used for each of the 0.5-, 1-, 2-, 4-, 8-, 10-, 12-, or 24-h exposure periods so that fish (N = 5 fish per container) being exposed for longer periods were not disturbed during sampling. Containers with exposure medium but no fish were used to assess metal losses, if any, due to adsorption to the plastic surface. The test medium was sampled at the beginning and end of the exposure period to measure metal levels as well as radioactivity.

Average metal concentrations in the exposure medium were not significantly different from nominal levels of 1 $\mu mol \cdot L^{-1}$ (0.97 ± 0.06, 0.95 ± 0.07, and 1.08 ± 0.05, for Cd, Cu, and Zn, respectively) but did decline slightly (1.2, 2.3, and 1.8% for Cd, Cu, and Zn, respectively) during the course of the 12- to 24-h exposures. This decline was due to absorption by the fish rather than adsorption by the walls of the polyethylene containers, for no corresponding decline was noted in containers to which no fish were added.

At the end of the exposure period, fish were removed, one at a time, rinsed in fresh hard water to remove any loosely bound surface metal, and killed with a single blow to the head. The tail was severed behind the anal fin and blood (≥0.25 mL) was collected from the cut surface into heparinized capillary tubes and centrifuged. Hematocrit, as well as volumes of whole blood, plasma, red blood cells (RBCs) and white blood cells (WBCs; white buffy coat on top of RBCs) were determined and, in some instances,

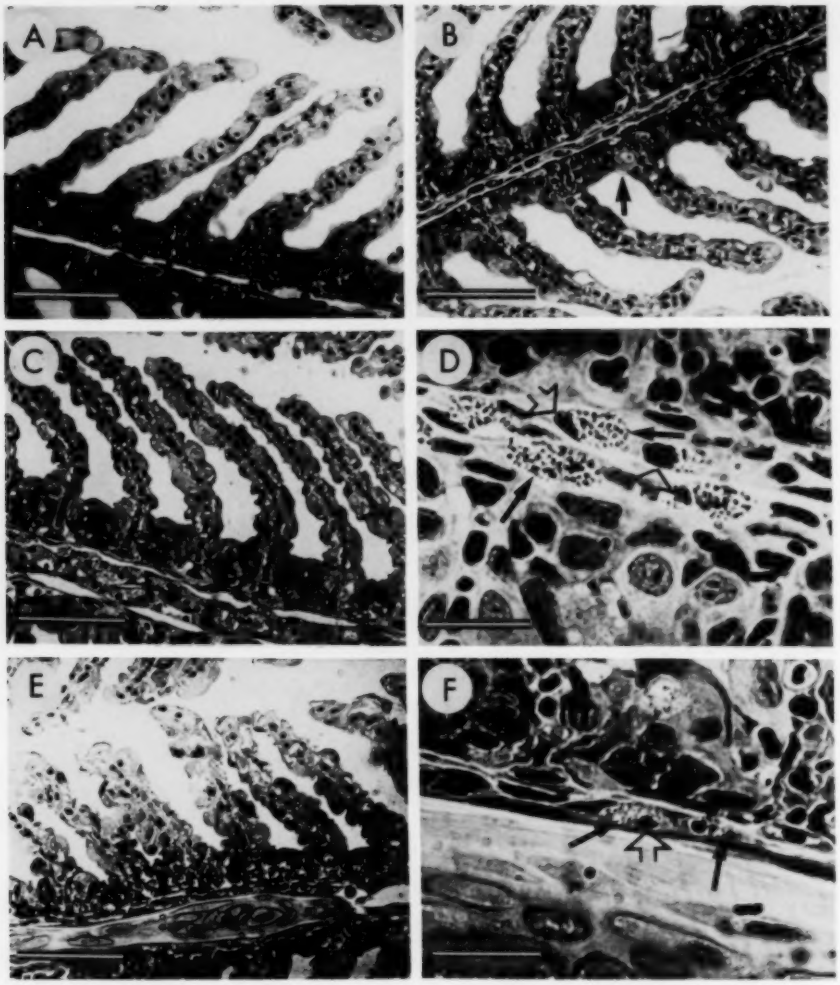

FIG. 1. Light micrographs of gills of rainbow trout. (A), (D), and (F) are from fish taken from holding tanks; (B) is from fish exposed for 24 h to Ca^{2+}-free water (i.e., no metal added); and (C) and (E) are from fish exposed for 24 h to 1 $\mu mol \cdot L^{-1}$ of Zn or Cd, respectively. Note an increase in surface roughness and lamellar thickness in (C) and (E) compared with (A) and (B). Chloride cells (B, arrow) were identified on the basis of their location, size of nuclei, and lightly staining cytoplasm. Granulocytes were identified on the basis of their location in the central sinus of filament (B and D), cytoplasmic grains (D, solid arrow), eccentric nuclei (D and F, open arrows), and absence of granular staining by PAS (F, solid arrows). Scale bars are 25 μm for (D) and (F) and 100 μm for the remainder. (A), (C), and (E) are stained with hematoxylin, (B) with methylene blue – basic fuschin, (D) with eosin and hematoxylin, and (F) with PAS.

plasma and RBCs were separated for radioactive counting. The whole gill basket was removed from the carcass and both tissues were weighed. Gill tissue, whole blood, plasma, RBCs and the remaining carcass were counted in a Packard Minaxi-5000 solid scintillation deep-well gamma counter with a 3 in. (1 in. = 2.54 cm) NaI crystal. Counts with samples containing ^{64}Cu were corrected for decay. Metal concentrations were verified using atomic absorption flame spectrophotometry on a Varian AAS (model 1275) against known standards.

Metal exposures for autoradiography

Fish (N = 4 per exposure) were exposed to each of the 1 $\mu mol \cdot L^{-1}$ metal solutions ($^{109}CdCl_2$, $^{65}ZnCl_2$) in Ca^{2+}-free medium for 24 h, or 100 $\mu mol \cdot L^{-1}$ $^{45}CaCl_2$ (N = 3) for 2 h under similar conditions as described above except with much higher specific activity (^{109}Cd, 18.7 $MBq \cdot \mu mol^{-1}$; ^{65}Zn, 9.4 $MBq \cdot \mu mol^{-1}$; $^{45}Ca^{2+}$, 0.5 $MBq \cdot \mu mol^{-1}$). Because all available radioisotopes of copper have a very short half-life (e.g., 12.9 h for ^{64}Cu), Cu autoradiography was not attempted.

Analytical Techniques

Tissue preparation for autoradiography

At the end of the exposure period, fish were removed, one at a time, briefly rinsed in hard water, and killed with a single blow to the head. The whole gill basket, liver, and

kidney were quickly dissected out and treated with 1% Na_2S in Sörensen buffer (pH = 7.4; Hayat 1981) for 10 min at 4°C prior to fixation. This treatment converts unbound Cd and Zn ions to insoluble metal sulfides, which then precipitate (Danscher 1981). Similarly, gill tissue from Ca^{2+} exposed fish were treated with a 4% solution of potassium pyroantimonate (Van Iren et al. 1979) to precipitate Ca^{2+} prior to fixation. Tissues from all treatments were fixed for 2 h in 2.5% phosphate buffered glutaraldehyde (pH = 7.4) at 4°C (Hayat 1981). After 1 h in fixative, the gill basket was dissected to individual arches and the second arch from the right-hand side was further cut into small pieces with a razor blade and all of the cartilage was removed. The tissues were counted at various stages for loss of radioactivity. Kidney and liver tissue were also cut into small pieces. Tissues were dehydrated in a graded ethanol series (50, 70, 80, 90, and 95%) for 1 h each, and infiltrated and embedded in JB4 resin (Polysciences Inc.) at room temperature. Sections (3 μm thick) were cut parallel to the filament and cross sectional to secondary lamellae using glass knives. Sections were transferred to glass slides and coated under dim light (Wratten-2 safelight filter) by the dipping method (Baker 1989) with Kodak NTB-2 nuclear track emulsion (Kodak Canada Inc.) diluted 1:1.5 with distilled water and maintained at 42°C. Slides were then stored at a 45° angle (section side up), allowed to dry for 2 h at room temperature, and then bleached in hydrogen peroxide vapors for 4 h. This treatment converts exposed silver grains, if there are any, back to silver bromide (the form reactive to light and radioactivity) and hence reduces background (Barber 1976; Kopriwa 1977). The slides were then transferred to a light-proof box with a dessicant and stored at 4°C for 2–4 wk for exposure. At the end of exposure period, the slides were developed for 2 min in Kodak D-19 developer, stopped in 1% acetic acid, fixed in Ilfospeed fixer (Ilford Photo Canada Ltd.), and washed in running tap water for 15 min. Slides were stained with hematoxylin and eosin (Humason 1967), cleared in xylene, and a cover glass mounted using DPX mounting medium (Fisher Scientific Co.). During analysis of label intensity, the tissue was focused first to identify the various cell types before the plane of focus was moved upward into the emulsion layer to count the number of silver grains. Autoradiographs were photographed with the label rather than the tissue in focus.

Autoradiography

Preliminary experiments on ^{65}Zn- and ^{109}Cd-exposed fish (for 4, 10, or 24 h) showed that 24 h was the minimum time needed to yield reliable labeling in various tissues and cells. Spatial resolution was relatively poor for shorter exposures because of lower label density as well as low signal-to-background ratio. For ^{45}Ca, 15-, 40-, and 120-min exposure periods were tested and 120 min yielded best results. All results reported are from fish exposed for 24 h to ^{65}Zn or ^{109}Cd and 2 h to ^{45}Ca. It was also determined that 2–3 wk was the best exposure time for emulsion after it was applied to sections. Label intensity was lower with shorter exposures.

Scanning electron microscopy

Scanning electron microscopy was performed for quantitative analysis of CC surface area expressed as a fraction of total surface area using techniques similar to those described by Laurent and Perry (1990). Five fish from each of the acclimation media were sampled, one at a time, and killed with a single blow to the head. The whole gill basket was quickly dissected out and fixed in 4% buffered gluteraldehyde (pH = 7.4) as described above. The second right arch from each fish was cut into individual filaments with a razor blade, rinsed six times, 30 min each, in phosphate buffer (pH = 7.4), dehydrated through a graded ethanol series (50, 70, 80, 90, 95, 100, and 100%) for 15 min each, and critical-point dried using CO_2. Dried filaments were glued on aluminum stubs using conductive silver paint. The tissue was oriented so that the lateral side of the filament was parallel with the stub surface. The stubs were then sputter coated with gold and examined with a Phillips 501 scanning electron microscope at 15 KV. The epithelial surface of the trailing edge near the base of the filament was viewed and photographed at approximately 3000× magnification. At least five noncontinguous fields from each fish were randomly chosen and photographed for subsequent morphometric measurements.

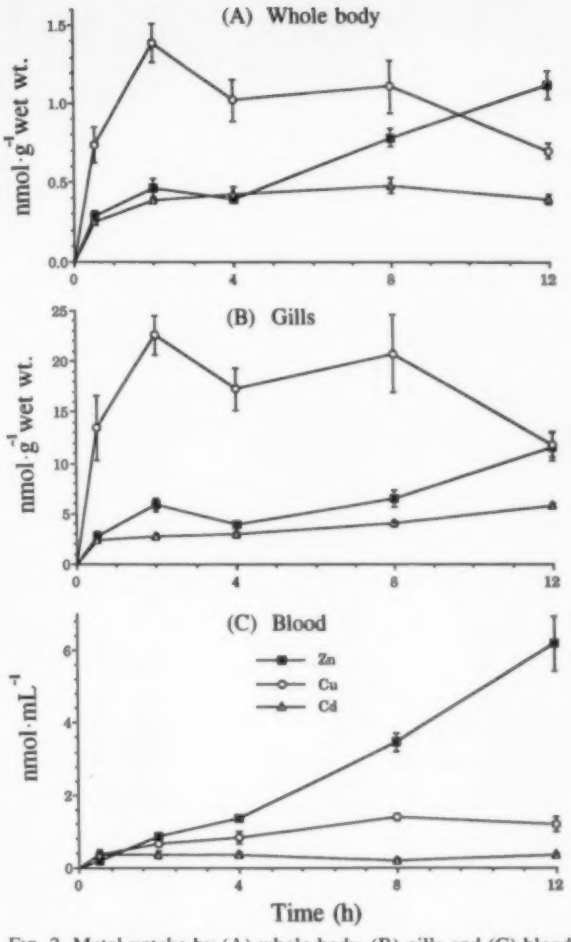

FIG. 2. Metal uptake by (A) whole body, (B) gills and (C) blood in hardwater-acclimated rainbow trout following exposure to 1 μmol·L^{-1} of Zn, Cu, or Cd in Ca^{2+}-free water for up to 12 h (mean ± SE, N = 5 per sample).

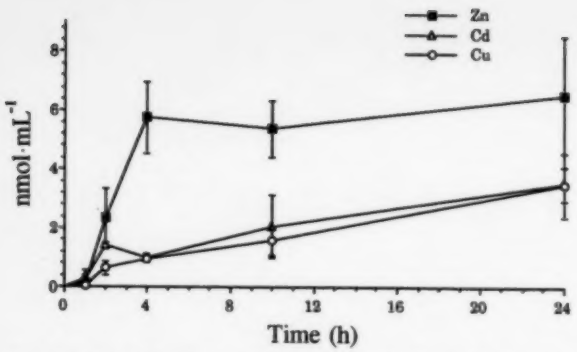

FIG. 3. Metal levels in white blood cells from hardwater-acclimated rainbow trout exposed to 1 μmol·L^{-1} of Zn, Cd or Cu in Ca^{2+}-free water for up to 24 h (mean ± SE, N = 5 per sample).

Histological and morphometric measurements

Autoradiograms were viewed and photographed using light microscopy (1000×) where the label (exposed and precipitated silver grains due to radioactivity) appeared as black dots. At least four gill sections from each fish (containing no less than 8 filaments each) were closely examined for label intensity. Counting was performed by using a grid type ocular micrometer precalibrated with a graduated stage micrometer (Bausch and Lomb Co.).

Gills from metal-exposed fish, fish exposed to Ca^{2+}-free water (see earlier for composition) and fish taken directly from hardwater holding tanks were also processed to identify various cell types and evaluate the effect of metal exposure. Slides were stained with hematoxylin, methylene blue – basic fuschin, or periodic acid – Schiff (PAS) counterstained with hematoxylin (Humason 1967). Chloride cells were identified on the basis of color of their cytoplasm as well as their location, size, and shape (Fig. 1B, arrow), while granulocytes were identified on the basis of their location, granular cytoplasm, eccentric nuclei (Fig. 1D), and their lack of staining with PAS (Fig. 1F) (Humason 1967).

Photographs of SEM images were scanned into a Macintosh SE computer with a hand-held scanner (Scanman, Logitech Inc.) and analysed for surface area using Canvas 2.1 (Denaba Software Inc.). A boundary was drawn around each of the chloride cells as well as the whole micrograph and the area within each boundary was determined. Areas were calibrated according to the scale bar on each photograph. The fractional chloride cell surface area for each fish was calculated by dividing the sum of total micrograph areas by the sum of individual chloride cell surface areas. Five frames from each fish (N = 5) were analyzed.

Calculations

The amount of metal in various tissues was estimated per gram (per milliliter in case of blood) of wet tissue according to

$$(1)\quad \text{Amount of metal (nmol}\cdot\text{g}^{-1}) = \frac{Q\text{SA}}{\text{tissue wet weight (g)}}$$

where Q is the radioactivity of the tissue in counts·min^{-1} (cpm) corrected for background and decay and SA is the specific activity of the exposure medium (nmol·cpm^{-1}). Whole body metal levels for each fish were calculated by adding amounts of metal present in various tissues counted separately.

TABLE 1. Metal uptake (nmol·mL^{-1}) by white blood cells (WBCs), red blood cells (RBCs), and plasma of trout after 10 h of exposure to 1 μmol·L^{-1} concentrations of Zn, Cu, or Cd (mean ± SE, N = 5 per sample).

Metal	WBCs	RBCs	Plasma
Zn	5.4±1.0	0.43±0.08	2.6±0.3
Cu	1.6±0.5	0.11±0.03	0.9±0.3
Cd	2.1±1.1	0.13±0.01	0.3±0.1

TABLE 2. Metal uptake by liver and kidney (nmol·g^{-1} wet tissue) of hardwater- acclimated fish after exposure to 1 μmol·L^{-1} of Zn, Cu, or Cd in low Ca^{2+} water for 24 h. Metal contents are also expressed as percent of total body burden (mean ± SE, N = 5 per sample).

	Metal levels			
Treatment	Liver	% of total	Kidney	% of total
Zn	2.37±0.38	2.29	2.22±0.2	1.44
Cu	17.73±1.31	21.83	2.39±0.28	1.41
Cd	1.48±0.15	3.48	1.91±0.14	1.47

Metal radioactivity in white blood cells (WBCs) were estimated by comparing plasma and RBC counts with whole blood counts and calculating missing counts (due to absence of WBCs from plasma and RBCs together) after correcting for hematocrit by using

$$(2)\quad Q_W = \frac{V_B\left\{Q_B - \left[\dfrac{Q_R Ht + Q_P(100 - Ht)}{100}\right]\right\}}{V_W}$$

where Q_W, Q_B, Q_R, and Q_P are cpm·mL^{-1} for WBCs, whole blood, RBCs, and plasma respectively, Ht is hematocrit and V_B and V_W are volumes of blood and WBCs in milliliters. Q_W was multiplied by SA (nmol·cpm^{-1}) to give metal concentrations in WBCs.

Statistical Analysis

All results reported are mean ± 1 SE. For CC surface area, results were analyzed by using one-way ANOVA and where there were significant treatment effects ($P < 0.05$), individual means were tested by Duncan's multiple range test ($P < 0.05$). Analysis for significance of difference for label density between chloride cells and rest of the epithelium was performed by using Student's t-test ($P < 0.05$).

Results

All fish survived up to 24 h of exposure to 1 μmol of Cu, Cd, or Zn in Ca^{2+}-free water (Ca^{2+} ~ 0.4 μmol·L^{-1}, Na^+ = 500 μmol·L^{-1}), whether the exposures were for analysis of metal uptake or for autoradiography. There was some evidence of gill damage in the metal exposed fish. This consisted of a small increase in lamellar thickness and an increased uneveness of the epithelial surface (Fig. 1C and E). There

TABLE 3. Comparison of metal uptake by whole body (WB) or gills (nmol·g^{-1} wet tissue) of hardwater (HW) and softwater (SW) acclimated fish after exposure to 1 μmol·L^{-1} of Zn, Cu, or Cd in low Ca^{2+} water for either 2 h or 12 h. Gill metal content is also expressed as a percentage of total body burden (mean ± SE, $N = 5$ per sample). *Significantly different from corresponding HW values ($P < 0.05$).

Treatment	Acclimation medium	Tissue	Metal exposure			
			2 h	% of total	12 h	% of total
Zn	HW	WB	0.5±0.1		1.1±0.1	
		Gills	5.9±0.7	47.6±2.4	11.7±1.3	37.8±2.4
	SW	WB	0.4±0.03		0.8±0.1*	
		Gills	2.8±0.5*	34.0±3.6	4.8±0.4*	24.6±0.8
Cu	HW	WB	0.4±0.03		0.6±0.07	
		Gills	22.6±1.4	66.2±2.1	11.9±1.3	49.9±3.3
	SW	WB	0.5±0.04		0.6±0.07	
		Gills	19.4±0.8	68.0±1.6	9.9±0.9	52.1±2.3
Cd	HW	WB	0.3±0.05		0.4±0.03	
		Gills	2.9±0.4	31.4±2.8	3.7±0.3	38.6±3.8
	SW	WB	0.8±0.02*		0.7±0.04*	
		Gills	8.8±1.3*	53.8±3.0	7.4±0.6*	54.7±2.5

was, however, no indication of either epithelial lifting or tissue necrosis, which are often reported for higher metal levels and more toxic exposures (Mallatt 1985). This moderate damage to gill tissue is apparently a consequence of metal exposure as it was not observed in fish either taken directly from hardwater holding tanks (Fig. 1A) or in fish exposed to Ca^{2+}-free water for 24 h (Fig. 1B).

Patterns of Metal Uptake

There was a very rapid initial whole-body uptake of Cd, Cu, and Zn (Fig. 2A). For Cu and Cd, this uptake had reached a plateau by 2 h whereas Zn uptake continued in an approximately linear fashion for the whole 12-h exposure period (Fig. 2A). By 12 h, the whole-body metal burdens were 1.1, 0.7, and 0.4 nmol·g^{-1} for Zn, Cu, and Cd, respectively. Uptake of the metal by the gill showed a similar pattern (Fig. 2B) but with somewhat larger differences amongst the metals. By 12 h, Zn, Cu, and Cd in the gills were 11.7, 11.9, and 3.7 nmol·g^{-1}, respectively, which represents 38, 50, and 39%, respectively, of the total radioactive-metal body burden. There was, nonetheless, a rapid transfer of metals across the external surface as each appeared quickly in the blood (Fig. 2C). For Zn, blood levels rose continuously throughout the 12 h exposure to reach 6.1 nmol·mL^{-1}, whereas Cu and Cd levels rapidly reached a plateau of 1.4 and 0.4 nmol·mL^{-1}, respectively. Within the blood compartment, most of the metal was contained in the plasma. At the end of 10 h, plasma contained 91, 92, and 80% of the total blood metal burden for Zn, Cu, and Cd, respectively. However, the WBCs had the highest metal concentrations (Table 1) with levels two to seven times higher than plasma. The loading of the WBCs with metal shows that this compartment rapidly loads Zn, reaching a plateau in 4–8 h (Fig. 3) while Cd and Cu levels continue to increase. After 24 h, Zn levels in WBCs were two times higher than for either Cu or Cd.

There was also a small but significant accumulation of metals by two key target organs, the liver and the kidney (Table 2). By 24 h, metal levels in kidney were ~2 nmol·g^{-1} for each of Zn, Cu, and Cd or about 1.4% of the total body burden. Levels of Zn and Cd in liver were similar (2.4 nmol·g^{-1} and 1.5 nmol·g^{-1} respectively) while Cu reached 17.7 nmol·g^{-1} and constituted over 21% of the total body burden.

Metal Uptake by Gills; Effect of Softwater Acclimation

The fractional CC surface area increased significantly after acclimation to soft water (SW), from $8.3 \times 10^4 \pm 0.7 \times 10^4$ μm^2·mm^{-2} in hard water (HW) acclimated fish to $21.8 \times 10^4 \pm 1.8 \times 10^4$ μm^2·mm^{-2} after 2 wk in soft water, a 2.6-fold increase, and remained at about the similar level ($20.9 \times 10^4 \pm 0.9 \times 10^4$ μm^2·mm^{-2}) for up to 4 wk. The gills of HW- and SW-acclimated fish accumulated anywhere from 25 to 55% of the whole-body total (Table 3) following 12 h exposure to either 1 μmol·L^{-1} Cu, Cd, or Zn. CC proliferation had no effect on Cu uptake. Whole body and gill metal levels were not significantly different between HW- and SW-acclimated fish after either the 2-h or 12-h exposure periods (Table 3). In contrast, SW acclimation significantly increased Cd uptake, and both whole body and gill Cd levels were two-fold higher in SW-acclimated fish than in HW-acclimated fish at the end of 12 h exposure. Zn uptake, on the other hand, showed the opposite trend (Table 3) with gill and whole body Zn uptake in SW-acclimated fish 50% lower compared with HW-acclimated fish.

Autoradiography

In situ localization of metals

With our precipitation techniques, total loss of radioactivity during processing for microscopy was no more than 25% up to the point of sectioning. Eighty percent of this loss occurred during fixation and washing of tissue with buffer, while the rest occurred during dehydration in ethanol. The loss of radioactivity may continue, even after sectioning, especially when sections are floated over warm water for flattening (Stirling and Kinter 1967). However, with the use of a very high radiospecific activity and histochemical precipitation, the tissue clearly contained sufficient radioactivity for analysis as indicated by excellent labeling resolution and density (Fig. 4).

Chloride cells were heavily labeled in fish exposed to 100 μmol·L^{-1} ^{45}Ca for 2 h (Fig. 4B, arrow). The amount of

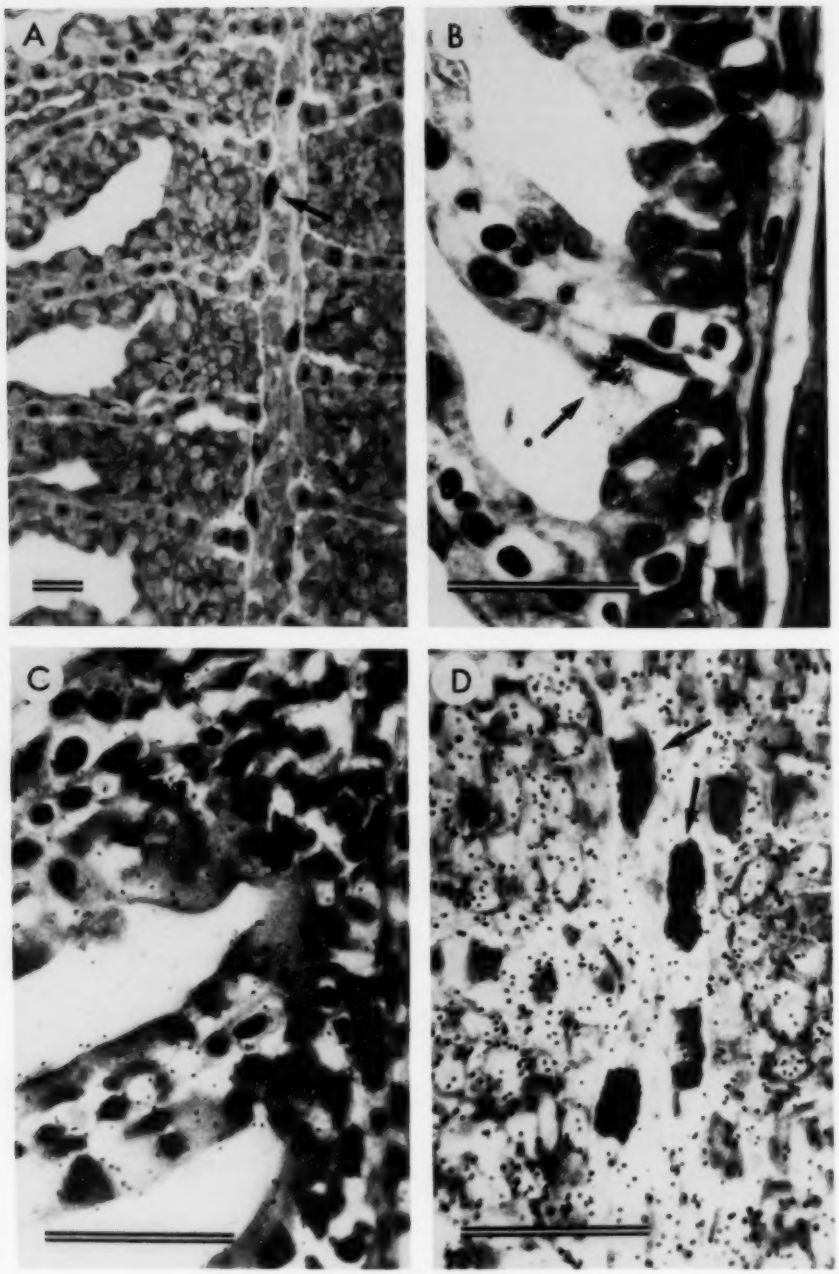

FIG. 4. Autoradiographic localization of ^{65}Zn, ^{45}Ca, and ^{109}Cd in gill tissue of rainbow trout after exposure to (A) 1 $\mu mol \cdot L^{-1}$ of ^{65}Zn for 24 h, (B) 100 $\mu mol \cdot L^{-1}$ of ^{45}Ca for 2 h, (C and D) 1 $\mu mol \cdot L^{-1}$ of ^{109}Cd for 24 h. Small arrows in (A) point to individual silver grains. In (A) and (D) note the dense areas of silver grains in the central sinuses of filaments (arrows) indicating uptake of Zn and Cd by granulocytes. Arrow in (D) indicates a chloride cells with high intensity of ^{45}Ca labeling. The higher label density in (C) and (D) versus (A) and (B) is due to the higher specific activity of ^{109}Cd versus ^{65}Zn or ^{45}Ca (18.7 $MBq \cdot \mu mol^{-1}$ vs. 9.4 $MBq \cdot \mu mol^{-1}$ and 0.5 $MBq \cdot \mu mol^{-1}$, respectively). Scale bar = 25 μm. Stain = hematoxylin.

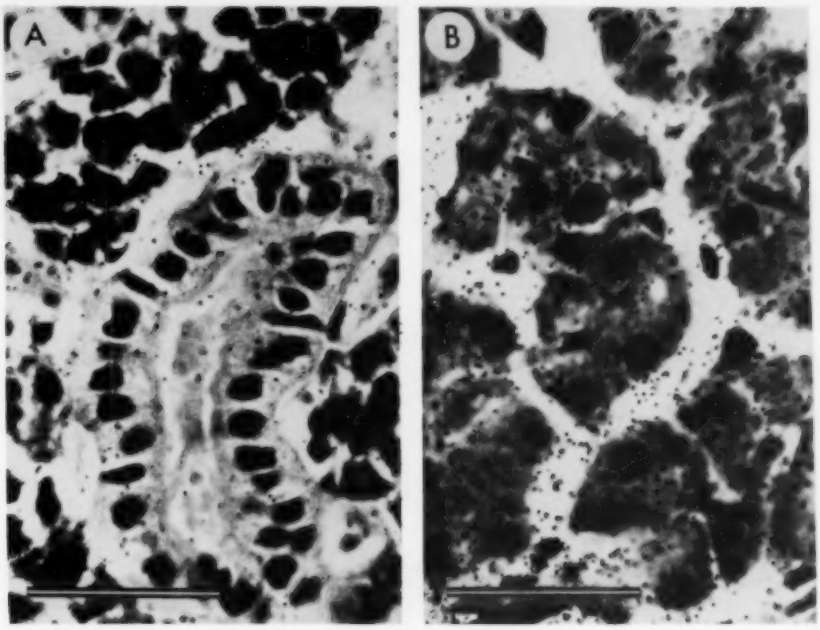

FIG. 5. Autoradiograms of (A) ^{65}Zn in the kidney and (B) ^{109}Cd in the liver after 24 h exposure to 1 $\mu mol \cdot L^{-1}$ of metals. Note the uniform distribution of label in both tissues. Scale bar = 25 μm. Stain = hematoxylin.

label was lower in the rest of the gill tissue but was uniformly distributed. In fish exposed to ^{65}Zn or ^{109}Cd for 24 h there was a no similar heavy labeling of CCs, instead the label was present in all of the epithelial cells (Figs. 4A and 4C, small arrows). Furthermore, a particular cell type, frequently located near the central sinus of the gill filament, was intensely labelled in both ^{109}Cd- and ^{65}Zn-exposed fish (Fig. 4A and 4D, arrows). These cells had a granular cytoplasm and were usually localized in the connective tissue adjacent to the filament cartilage but were also observed inside lamellar blood channels in both controls and ^{65}Zn- and ^{109}Cd-exposed fish. Cytoplasmic granules in these cells stained with hematoxylin and eosin (Fig. 1D) but remained unstained with PAS and hematoxylin (Fig. 1F), which identifies these cells as eosinophilic granulocytes (Baker 1976; Humason 1967).

Zinc and Cd were also localized in kidney and liver cells by autoradiography (Fig. 5). The label was uniformly distributed in the liver (Fig. 5A) and the kidney (Fig. 5). In the kidney the label was also frequently associated, at a higher density, with apparently precipitated material. These randomly scattered precipitates, present in the interstitial tissue, appeared after the tissue was treated with Na_2S and probably consist of insoluble sulfides of various divalent ions (Danscher 1981).

Quantitative analysis of autoradiographs

The average background level for silver grains was estimated to be $5.6 \times 10^{-3} \pm 0.9 \times 10^{-3}$ grains$\cdot \mu m^{-2}$ (i.e., silver grains not associated with tissue). Within the tissues, the label density ranged from 3.4× higher than background in kidney cells (1.9×10^{-2} grains$\cdot \mu m^{-2}$) in ^{65}Zn-exposed fish to 113× higher than background in granulocytes in Cd-exposed fish. In ^{109}Cd-exposed fish the lowest label density was found in kidney tissue (3.0×10^{-2} grains$\cdot \mu m^{-2}$) while granulocytes had the highest density (103.4×10^{-2} grains$\cdot \mu m^{-2}$; Fig. 6A). Similar to ^{109}Cd ^{65}Zn label density was lowest in kidney tissue (1.9×10^{-2} grains$\cdot \mu m^{-2}$) and highest in granulocytes (46.5×10^{-2} grains$\cdot \mu m^{-2}$; Fig. 6B). For both ^{109}Cd- and ^{65}Zn-exposed fish the difference in label intensity among pavement cells and chloride cells was not significant (Fig. 6). However, in ^{45}Ca-exposed fish, label intensity was significantly higher ($P < 0.05$) in CCs than pavement cells (Fig. 6). Unlike ^{109}Cd and ^{65}Zn, ^{45}Ca did not accumulate in granulocytes.

Discussion

Our results confirm that the gills are an important route of metal uptake and also illustrate that, in the initial stages of metal exposure, the gills retain most of the metal burden (Fig. 2A and 2B; Table 3), thus suggesting that gill metal levels can be used to assess the severity of acute metal exposure. For each metal, more than half of the total metal burden in the gills was attained within the first 30 min of exposure (Fig. 2B). This reflects surface absorption rather than true uptake as the appearance of metals in the blood was over a much longer time course (Fig. 2C). Indeed, it appears that metal uptake by the gills does not involve direct and rapid transfer from the water to the blood, but rather an intermediate step where the metals first accumulate in the gill tissue. By 12 h this accumulation had reached levels 3 to 11-fold higher than the environment (i.e., gill levels of 3–11 nmol$\cdot g^{-1}$ at 12 h vs. water levels of 1 nmol$\cdot mL^{-1}$; Fig. 4B).

Uptake of Calcium

Chloride cells were distinctly labeled with ^{45}Ca (Fig. 4B) with a significantly higher label density compared with other

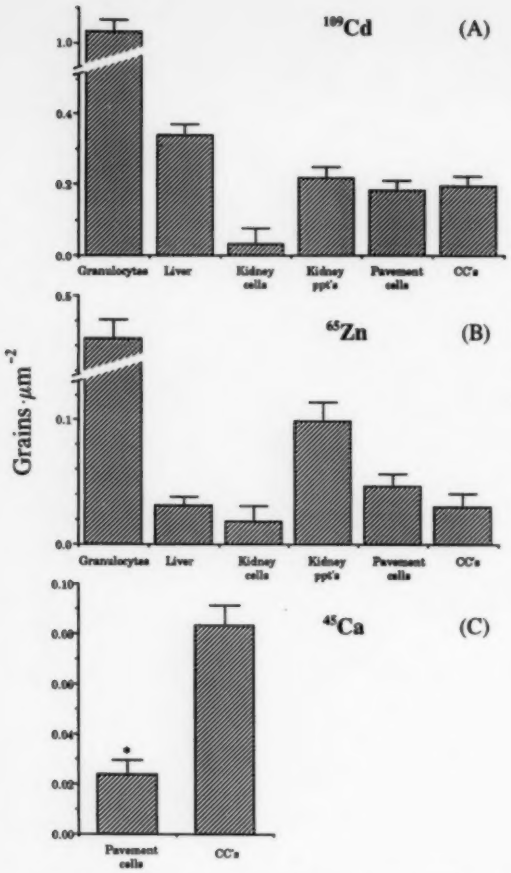

FIG. 6. Quantitative analysis of autoradiograms from various tissues from fish exposed to (A) 1 $\mu mol \cdot L^{-1}$ of ^{109}Cd, (B) 1 $\mu mol \cdot L^{-1}$ of ^{65}Zn or (C) 100 $\mu mol \cdot L^{-1}$ of ^{45}Ca. CCs = chloride cells; ppts = precipitates. Asterisk in (C) indicates significant difference (*t*-test, $P < 0.05$) between pavement cells and CCs (mean ± SE, $N = 12–15$).

epithelial cells (Fig. 6C) suggesting that ^{45}Ca is selectively taken up by these cells. This is essentially the same finding as that reported by Ishihara and Mugiya (1987) where, with the help of electron microscopy, they observed oxalate-induced Ca^{2+} precipitates only in CCs and not in other branchial epithelial cells in goldfish, *Carassius auratus*. The importance of this finding to the present study is that it suggests that any metal that transits the gills should be detectable in epithelial cells using autoradiographic techniques.

Uptake of Metals

Two independent lines of evidence point to the conclusion that CCs are not, in fact, an important route for metal uptake in the gills. Firstly, the autoradiography studies showed that Cd and Zn were not concentrated by CCs. Instead, the distribution of the label was such to suggest that Cd and Zn permeate nondiscriminately through the general epithelial surface. Secondly, softwater acclimation did not increase the uptake of either Cu or Zn despite the doubling of CC fractional surface area.

Softwater acclimation, in addition to provoking CC proliferation, also brings about a variety of changes in the gills that act to increase Ca^{2+} uptake, including an increase in gill surface Ca^{2+} binding (both affinity and capacity; Reid 1989), increases in calmodulin content of mucus (Flik et al. 1984), increased branchial Ca^{2+}-ATPase activity (Flik and Perry 1989), and an increase in the affinity and capacity of the Ca^{2+} transport mechanism (Perry and Wood 1985).

The absence of a stimulation of Cu uptake by SW acclimation is perhaps not surprising because Cu exhibits only a limited interaction with Ca^{2+}. It is only slightly inhibitory of Ca^{2+} uptake (Reid and McDonald 1991) and increasing Ca^{2+} in the water does not inhibit Cu influx (Laurén and McDonald 1987).

The absence of an increase in Zn influx with SW acclimation is, however, somewhat puzzling in view of the known interactions between Zn and Ca^{2+} uptake (Spry and Wood 1989; Hogstrand et al. 1994) and a previous study by Spry and Wood (1988) which showed an increase in Zn influx in the rainbow trout after acclimation to softwater. However, it is important to emphasize that the present study examined Zn uptake at much lower levels than previous studies (e.g., 1 $\mu mol \cdot L^{-1}$ vs. 25–30 $\mu mol \cdot L^{-1}$ in Spry and Wood 1988). It is also surprising to find that Zn influx was actually significantly lower in SW- versus HW-acclimated animals. The decrease in Zn influx, however, was specifically the effect of the low Ca^{2+} in the exposure medium (~0.4 $\mu mol \cdot L^{-1}$) rather than SW acclimation per se because Zn influx was not significantly different between SW- versus HW-acclimated fish at higher levels of Ca^{2+} in the water (0.1 and 1.0 $mmol \cdot L^{-1}$; S. Zia, unpublished results).

Nonetheless, the absence of an increase in Zn uptake by an epithelium adapted for increased Ca^{2+} uptake and in an environment virtually free from Ca^{2+} suggests that Zn uptake is not exclusively via Ca^{2+} channels in the apical membrane or even via Ca^{2+} binding ligands at least when Zn levels in the water are ≤1 $\mu mol \cdot L^{-1}$. Under these circumstances we conclude that the Zn uptake is via a distinctly different mechanism but its nature at present is uncertain.

In contrast, there was a pronounced stimulation in Cd uptake with SW acclimation. This finding is in agreement with previous studies reporting a strong affinity of Cd for Ca^{2+} binding ligands and interactions between Cd and Ca^{2+} transport. For example, the affinity of Ca^{2+}-ATPase in rainbow trout is at least 100 times higher for Cd than for Ca^{2+} (Verbost et al. 1988) and stanniocalcin, which is important for Ca^{2+} homeostasis in fish and limits branchial Ca^{2+} uptake, also inhibited Cd uptake (Verbost et al. 1989a). Therefore, we support the view of Verbost et al. (1989b) that Cd uptake in fish involves entry through apical Ca^{2+} channels, binding to intracellular proteins, and then diffusing through the basolateral membrane. The corresponding inhibition of Ca^{2+} uptake occurred, the authors argue, because of Cd's inhibition of Ca^{2+}-ATPase on the basolateral membranes. However, our finding that Cd does not specifically accumulate in CCs also suggests (in contrast to Verbost et al. 1989b) that Ca^{2+} channels are not confined solely to CCs and/or that Cd passes through nonspecific channels present on pavement cells. Although the CCs appear to be the primary cells responsible for Ca^{2+} transport (Perry and Wood 1985; Perry and Flik 1988) the presence of Ca^{2+} channels and Ca^{2+} transport in pavement cells cannot be ruled out (Perry and Wood 1985).

Metal Uptake by Granulocytes

The presence of dense labelling on the eosinophilic granulocytes within gill tissue (Fig. 4A, 4D, and 6) as well as inside the blood channels of the secondary lamellae indicates an enormous capacity of these cells to accumulate both Cd and Zn (at least 6 and 10 times higher, respectively, than any other gill epithelial cells; Fig. 6). However, when compared with the total metal levels in gills (Fig. 2), metal levels in the white blood cell fraction of the blood (5.4 and 2.1 $nmol \cdot mL^{-1}$ for Zn and Cd, respectively; Table 2) at the end of the 10-h exposure period were actually lower than the respective metal levels in whole gill tissues (11.7 and 3.7 $nmol \cdot g^{-1}$; Fig. 2B). This discrepancy can be explained with the observation that, in teleosts, granulocytes comprise only 3–8% of the total white blood cell population (Ellis 1977). Assuming that granulocytes are the only cells involved in metal accumulation, their dilution by other cells would have resulted in lower metal levels in the WBC compartment.

The exact role played by these cells in Cd and Zn metabolism is not known at present. However, Powell et al. (1990) have recently shown that granulocytes migrate through blood capillaries within the gill tissue of rainbow trout and suggest that this migration aids in immunological or defense mechanisms. Furthermore, Baatrup (1989), using a silver enhancement method, found that the eosinophilic granule cells in the gills had high levels of endogenous Zn relative to other gill cells. In humans, Harley et al. (1989) reported induction of metallothionein in lymphocytes and monocytes after in vitro exposure to cadmium chloride. From the present study, it is difficult to conclude whether these cells are accumulating more metals or simply replacing an endogenous metal pool with radioactive metals. However, it seems possible that these cells might be taking part in detoxification of Cd and Zn by accumulating metal ions in high quantities and thus making them unavailable to surrounding cells.

Metal Uptake by Other Tissues

The autoradiographic localization of ^{109}Cd and ^{65}Zn in the liver and the kidney (Fig. 5) not only verifies the usefulness of our techniques for localizing metals but also confirms that there is an uptake of these metals through the gills and a subsequent transport by the blood to these organs. In the kidney tissue there were patches of precipitated material (owing to Na_2S treatment), densely labeled with both ^{109}Cd and ^{65}Zn, localized in the interstitial area. Similar patchiness was also observed at the organ level by Tjälve and Gottofrey (1986) and Karlsson-Norrgren (1985) during autoradiographic localization of ^{109}Cd. These observations suggest that interstitial cells rather than tubules are the sites of metal deposition. In liver, in contrast, all cells were labeled more or less uniformly. These observations suggest that despite significant metal accumulation by these tissues (~2% of body burden per tissue; Table 2) there is no target cell in either tissue. Because both tissues have been implicated in the excretion of metals (in urine, Tjälve and Gottofrey 1986; in bile, Baatrup 1989; Lanno et al. 1987) our results suggest that excretion may not be associated with specific metal accumulation in the relevant cells (tubule cells in kidney; hepatic cells lining the bile canaliculi in liver). However, it may be that activation of excretion mechanisms may take longer than the 24-h exposure period employed here. Clearly, longer metal exposure times, and higher resolution microscopy is required to resolve this issue.

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The Harmful Phytoplankter *Chaetoceros concavicornis* Causes High Mortalities and Leucopenia in Chinook Salmon (*Oncorhynchus tshawytscha*) and Coho Salmon (*O. kisutch*)

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Chaetoceros concavicornis is a harmful phytoplankter that occurs in many temperate coastal seawaters and can cause fin fish mortalities when present at concentrations as low as 5 cells·mL^{-1}. At even lower concentrations, this diatom can stress salmonids to such an extent that they may express a disease to which they are most prone at the time of *C. concavicornis* exposure. We report mortality rates of coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) exposed to different concentrations of *C. concavicornis*. Our data indicate that in the presence of harmful concentrations of *C. concavicornis*, blood hematocrit and erythrocyte, glucose, and lactate concentrations of yearling chinook salmon (*O. tshawytscha*) increase. The microridges of the primary lamellae decreased in prominence in the presence of harmful concentrations of this phytoplankter, while the goblet cells became more prominent and more numerous. Neutrophil, lymphocyte, and thrombocyte concentrations in the blood became depleted. These data suggest that suppression of a portion of the chinook's immune system is occurring which may partially explain the earlier observation that salmonids cultured in the presence of harmful *C. concavicornis* phytoplankton became more susceptible to disease, including *Vibrio* infections.

Chaetoceros concavicornis est un organisme phytoplantonique nuisible qui vit dans bon nombre d'eaux de mer côtières tempérées et qui peut entraîner de la mortalité chez les poissons s'il est présent à des concentrations aussi faibles que 5 cellules par mL. À des concentrations encore plus faibles, cette diatomée peut provoquer chez les salmonidés un stress tel qu'ils peuvent exprimer une maladie à laquelle ils sont les plus susceptibles au moment de l'exposition à *C. concavicornis*. Nous signalons ici les taux de mortalité du saumon coho (*Oncorhynchus kisutch*) et du saumon quinnat (*O. tshawytscha*) exposés à diverses concentrations de *C. concavicornis*. Nos données indiquent qu'en présence de concentrations nuisibles de *C. concavicornis*, l'hématocrite, la numération érythrocytaire et les concentrations de glucose et de lactate ont augmenté chez le saumon quinnat (*O. tshawytscha*) de 1 an. En présence de concentrations nuisibles de cet organisme phytoplanctonique, les microstries de la lamelle primaire ont perdu en proéminence alors que les cellules caliciformes sont devenues plus proéminentes et plus nombreuses. Les concentrations sanguines de neutrophiles, de lymphocytes et de thrombocytes ont diminué. Ces données indiquent une immuno-suppression d'une partie du système immunitaire du saumon quinnat qui peut expliquer, du moins en partie, l'observation antérieure selon laquelle les salmonidés cultivés en présence de l'organisme phytoplanctonique nuisible *C. concavicornis* deviennent plus susceptibles aux maladies, y compris aux infections à *Vibrio*.

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Previous research has shown that the spined (with barbs) diatoms *Chaetoceros concavicornis* and *C. convolutus* are overtly lethal to salmonids at concentrations in excess of approximately 5 cells·mL^{-1} (Bell et al. 1974). Albright et al. (1993) subsequently showed that at several sites along the coast of British Columbia, *C. concavicornis* and *C. convolutus*, at concentrations less than 5 cells·mL^{-1}, may exacerbate mortality rates of penned salmonids due to other diseases such as vibriosis and bacterial kidney disease.

Yang and Albright (1992) have shown that spined and barbed cells of *C. concavicornis* irritate the goblet cells of the respiratory epithelium of rainbow trout (*Oncorhynchus mykiss*) such that there is an overproduction and accumulation of mucus on the primary and secondary lamellae. This mucus inhibits oxygen uptake by the respiratory epithelium and the blood becomes hypoxic. If the blood becomes sufficiently hypoxic, the fish dies. These authors also found that the increase in blood glucose and lactate concentrations as well as in hematocrit values of trout exposed to lethal concentrations of *C. concavicornis* in the surrounding water are characteristic of finfish undergoing anaerobiosis.

Because harmful concentrations of *C. concavicornis* have such a marked influence on several blood parameters of the rainbow trout, we felt that a more thorough investigation was warranted: (1) to determine the mortality rates of coho salmon (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) exposed to different concentrations of *C. concavicornis*, and (2) to determine the influence of this phytoplankter on blood leucocyte concentrations with special reference to neutrophils, lymphocytes, and thrombocytes.

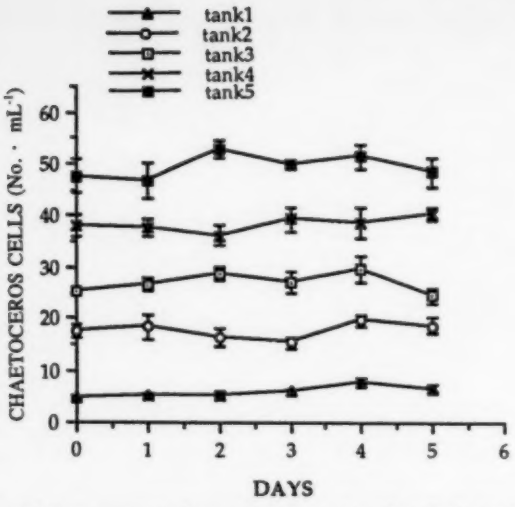

FIG. 1. Mean concentrations of *C. concavicornis* cells in treated tanks 1, 2, 3, 4, and 5 in experiment 1. Error bars indicate ±SE.

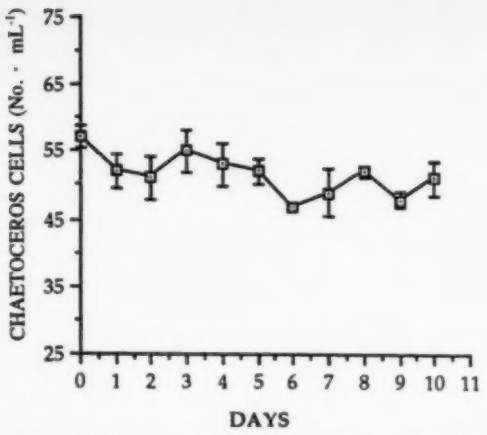

FIG. 2. Mean (of three trials) concentration of *C. concavicornis* cells in treated seawater. Error bars indicate ±SE.

Materials and Methods

Culture

Chaetoceros concavicornis was obtained from the Northeast Pacific Culture Collection at the Department of Oceanography, University of British Columbia. This culture was originally isolated from a bloom at Jericho Beach, Vancouver, B.C. *Chaetoceros concavicornis* was cultured using Harrison's medium (Harrison et al. 1980). Two-litre volumes, which initially contained approximately 100 cells·mL^{-1} of *C. concavicornis*, were cultured in a Fernbach flask for 2 wk. The temperature and photoperiod were approximately 14°C and 14 h light : 10 h dark, respectively. To determine concentrations of *C. concavicornis*, 2- or 10-mL portions of the cultures were prestained with 4,6-diamidino-2-phenylindole (DAPI) and counted using the technique of Porter and Feig (1980).

Experiment 1

This experiment was carried out using 9- to 18-g coho salmon obtained from Capilano Fresh Water Fish Hatchery in West Vancouver, B.C. All fish were transported to Simon Fraser University in aerated, 20‰ salinity water and held under these conditions for more than 1 mo prior to use.

Three-hundred coho were randomly divided into six groups of 50 fish each and placed in separate 200-L tanks. The salinity, pH, temperature, and dissolved oxygen of the water were 20‰, 7.2–7.8, 12.5–13.5°C, and 8.2–10.2 mg·L^{-1}, respectively, during the experiment.

The water in tanks 1, 2, 3, 4, and 5 was treated daily with *C. concavicornis*, to achieve concentrations of 4–6, 15–19, 24–29, 36–40, 46–52 cells·mL^{-1}, respectively, during the experiment (Fig. 1). Tank 6 served as the untreated control.

Throughout the experiment, dead and/or moribund fish were removed and the mortality rates were calculated (moribund fish were treated as dead).

Experiment 2

Yearling chinook salmon of 4.8-g mean weight and 8.9-cm mean fork length were provided by the Pacific Biological Station, Canada Department of Fisheries and Oceans, Nanaimo, B.C. The fish were transferred to the Aquatic Facility at Simon Fraser University where they were held for at least 4 wk in fresh water at 9.5–10.5°C, dissolved oxygen content of 9.3–9.8 mg·L^{-1} and pH 5.8–6.5 until used for experimental purposes. The fish were fed a commercial pellet salmon food daily.

Two weeks prior to each of three replicate experiments, a group of 50 fish was placed in each of two, 200-L oval culture tanks. Each tank contained 100 L of aerated seawater, approximately 20‰ salinity. The temperature, dissolved oxygen, and pH ranges during the course of each experiment were 10.5–11°C, 8.1–10.1 mg·L^{-1}, and 7.3–7.9, respectively. The water in each tank was changed once daily between 19:00 and 20:00.

During the course of each experiment the fish in tank 1 were continuously exposed to between 47 and 57 cells·mL^{-1} *C. concavicornis* (Fig. 2). The fish in tank 2 were not exposed.

Throughout each experiment, dead and moribund fish were removed each morning, weighed, and fork lengths measured. Where appropriate, the gills of selected moribund fish were dissected out and preserved in 3% glutaraldehyde for light and scanning microscopy.

At days 1, 3, 5, and 10 following the initiation of each experiment, 10 live fish were randomly selected and removed from each tank and immediately placed in 20‰ salinity seawater containing the anaesthetic, 2-phenoxyethanol (0.4 mL·L^{-1}). When anesthetized, each fish was removed, weighed, and the fork length measured. Blood samples were taken by sectioning the caudal peduncle and collecting the blood in heparinized microcapillary hematocrit tubes.

Total blood cell counts were determined as described by Pickering (1986) and Pickering and Pottinger (1985, 1987). Five-microlitres aliquots of each blood sample were diluted in 1% NaCl solution (final dilution 1 : 40 000), fixed in Lugol's iodine and counted using Utermohl (1958) chambers and an inverted microscope. The total number of blood cells within each of fifteen 1-mm^2 grids was counted with the aid of an ocular grid. The mean of the 15 values was then related to the total area of the Utermohl chamber.

Differential cell percentage counts were made from air-dried, methanol-fixed, stained (hematoxylin and eosin) blood

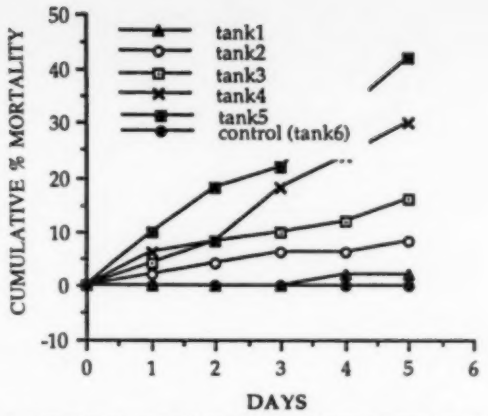

FIG. 3. Cumulative mortalities of coho salmon exposed to *C. concavicornis* in tanks 1, 2, 3, 4, and 5 and untreated controls (tank 6).

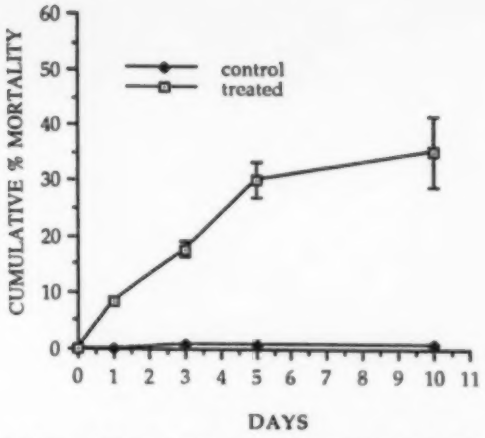

FIG. 4. Mean (of three trials) cumulative mortalities of chinook salmon exposed to *C. concavicornis* and untreated controls. Error bars indicate ±SE.

smears. All cells within ten 1-mm^2 grids of each smear were counted using a light microscopy. Absolute concentrations of erythrocytes, lymphocytes, neutrophils, and thrombocytes were then calculated from the total and differential blood counts (Pickering 1986; Pickering and Pottinger 1985, 1987).

For scanning electron microscopy (SEM) each whole gill was fixed in 3% glutaraldehyde, post-fixed in 1% OsO_4, dehydrated in ethanol and amyl acetate, critical point dried, and gold coated. Material prepared in this way was examined using an Autoscan SEM.

For analysis of plasma glucose and lactate, blood was centrifuged at 2000 rpm for 8 min. The resulting plasma was stored at −20°C until analyzed for glucose concentrations using a Sigma Chemical Co. (St. Louis, MO) diagnostic kit. The assay is based on enzymatic phosphorylation of glucose by hexokinase and oxidation by glucose-6-phosphate dehydrogenase. Plasma lactate levels were determined using a Sigma diagnostic kit. The assay is based on a single enzymatic oxidation of lactate.

The data from all three experiments are presented as the means ± SE for each parameter assayed. Values for hematocrits, blood cell counts, and glucose and lactate concentrations were analyzed for differences of each variable between control and treated fish using Student's *t*-test.

Results

Experiment 1: Cumulative Mortality Rates of Coho Salmon Exposed to *C. concavicornis*

No fish died in the untreated control group (tank 6) during the course of the experiment, whereas a total of 1, 4, 8, 15, and 21 fish died in tanks 1, 2, 3, 4, and 5, respectively. The data were pooled and presented as cumulative mortalities. The mean cumulative mortality rates of the fish in tanks 1, 2, 3, 4, and 5 were 2, 8, 16, 30, and 42%, respectively, within 5 d of treatment (Fig. 3).

Experiment 2: Cumulative Mortality Rates of Chinook Salmon Exposed to *C. concavicornis*

The mean cumulative mortality rates were calculated by the formula, $Z_n = (\ln N_T - \ln N_t)/(t - T) + Z(n - 1)$, where Z_n is cumulative mortality of fish at n day(s); N_T and N_t are the numbers of fish at T and t days, respectively; T is the day fish were first sampled; t is the day fish were next sampled; and $Z(n - 1)$ is the cumulative mortality of fish at $n - 1$ days. The mean cumulative mortality of the fish exposed to *C. concavicornis* was approximately 35% after 10 d of treatment. The mortality of the untreated control fish was 0.60% (Fig. 4).

Scanning Electron and Light Microscopy

Fish treated with *C. concavicornis* had many barbed spines trapped in the inter-secondary and primary lamellar spaces (Fig. 5A). The goblet cells of the primary lamellae of the treated fish (Fig. 5C) were larger and more numerous than those of the untreated control fish (Fig. 5B). The well-defined microridges present on the primary lamellae of the untreated control fish (Fig. 5B) were much less prominent following 24 h of exposure of the fish to *C. concavicornis* (Fig. 5C). Histological examination shows that some of the spines of *C. concavicornis* became imbedded in the tissues of the secondary lamellae (Fig. 5D). Necrosis and exfoliation of secondary lamellae cells and congestion in the capillaries of the gills of chinook salmon exposed to *C. concavicornis* for 48 h were observed (Fig. 5E).

Plasma Glucose Concentration

The plasma glucose concentration of the treated fish greatly increased from 57.0 mg·dL^{-1} immediately prior to *C. concavicornis* treatment to 83.8 mg·dL^{-1} within 72 h of treatment. After 72 h, the mean glucose concentrations gradually decreased (Fig. 6). At time 0, the mean glucose concentration in the plasma of the untreated control fish was 56.0 mg·dL^{-1} and remained approximately the same during the 10-d experiment. The plasma glucose concentrations in the treated fish were significantly different from those of the untreated control fish at day 1 ($p < 0.05$), day 3 ($p < 0.05$), day 5 ($p < 0.01$), and day 10 ($p < 0.05$).

Plasma Lactate Concentration

The plasma lactate concentration of the treated fish increased from 30.1 to 51.7 mg·dL^{-1} during the 10-d

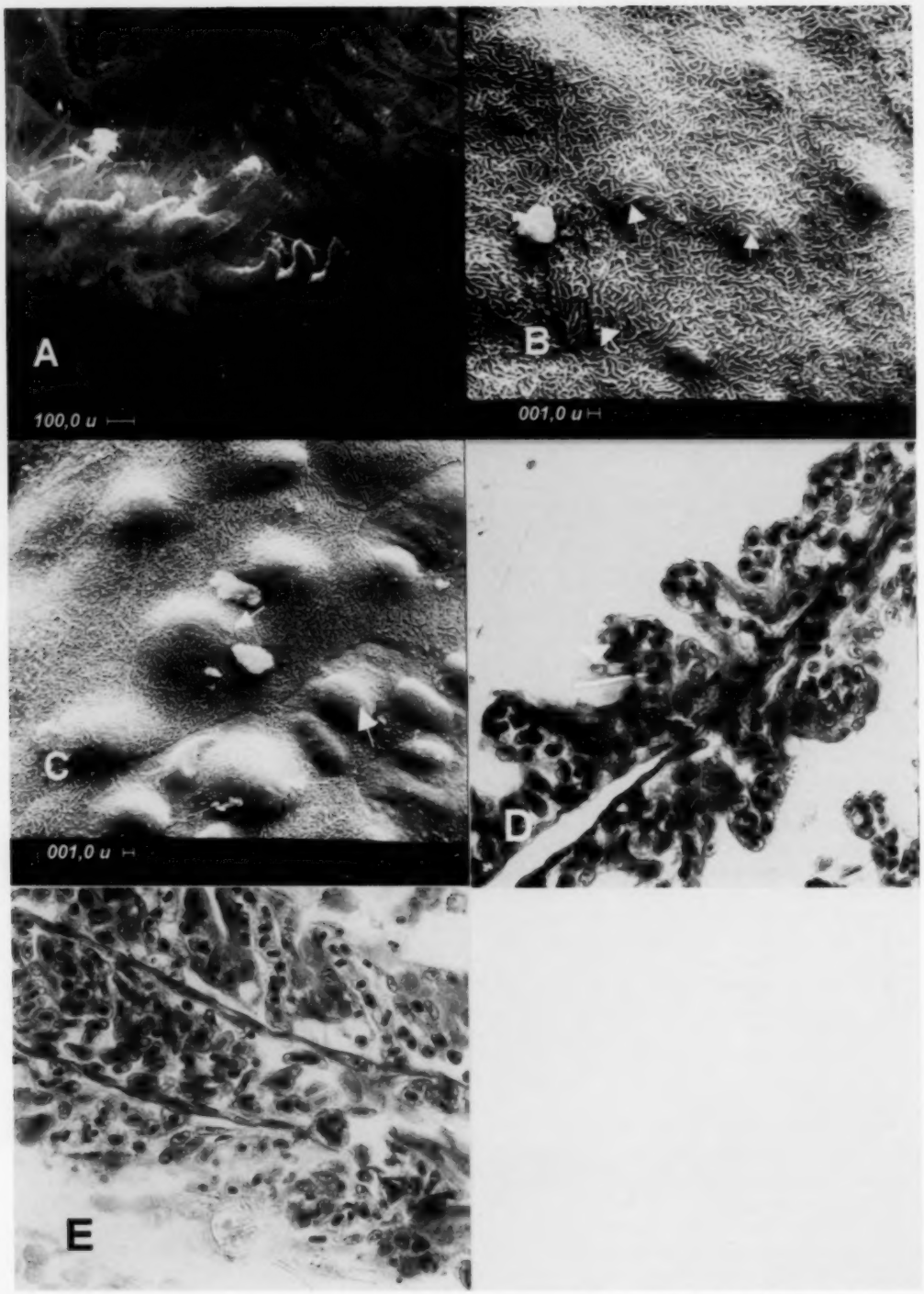

FIG. 5. Scanning electron microscopic views of (A) yearling chinook exposed to *C. concavicornis* with many barbed spines trapped in the intersecondary and primary lamellae. (B) Goblet cells (arrow) and microridges present on the primary lamellae of untreated chinook. (C) Goblet cells (arrow) and microridges present on the primary lamellae of chinook salmon exposed to *C. concavicornis*. Light microscopic views of (D) a spine of *C. concavicornis* imbedded into the tissue of secondary lamellae (hematoxylin and eosin staining 300×); (E) necrosis and exfoliation of secondary lamellae cells and congestion in the capillaries of gill in chinook salmon exposed to *C. concavicornis* for 48 h (hematoxylin and eosin staining 240×).

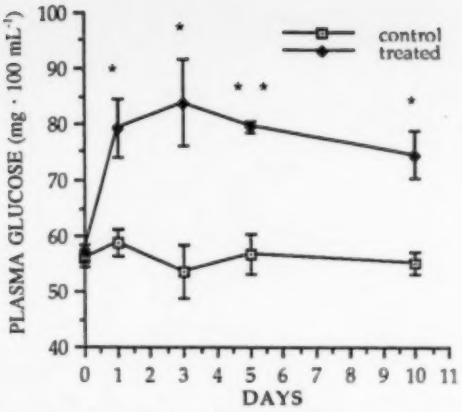

FIG. 6. Mean (of three trials) plasma glucose concentrations of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE. * and ** indicate significant differences ($p < 0.05$ and $p < 0.01$), respectively.

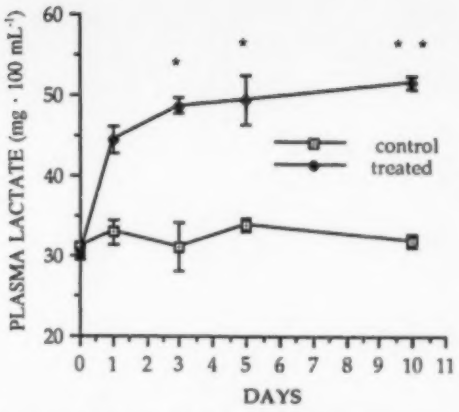

FIG. 7. Mean (of three trials) plasma lactate concentrations of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE. * and ** indicate significant differences ($p < 0.05$ and $p < 0.01$), respectively.

treatment (Fig. 7). The mean lactate concentrations in the blood of the untreated fish remained within the range of 31.3–33.8 mg·dL^{-1} during the 10-d treatment. The plasma lactate concentrations in the treated fish were significantly different from those of the untreated control fish at day 3 ($p < 0.05$), day 5 ($p < 0.05$), and day 10 ($p < 0.01$).

Hematocrit Values

Immediately prior to *C. concavicornis* treatment the mean hematocrits of the treated and untreated fish were 37.0 and 37.8%, respectively. Following treatment, the hematocrit in the treated fish increased to a mean of 47.2% within 24 h (Fig. 8). The hematocrit in the untreated fish showed a minor increase at 24 h followed by a slow decline to day 10. Although the hematocrit in the treated fish decreased somewhat following the sharp rise at 24 h, the values in the treated fish remained above those of the control fish over the 10-d experimental period. The hematocrits in the treated fish were significantly different from those of the untreated control fish at day 1 ($p < 0.001$), day 3 ($p < 0.01$), day 5 ($p < 0.05$), and day 10 ($p < 0.05$).

Blood Erythrocyte Concentrations

Immediately prior to *C. concavicornis* treatment the mean counts of erythrocytes in the blood of the treated and untreated fish were 764 × 10^3 and 776 × 10^3 μL^{-1}, respectively. While the concentrations of erythrocytes remained approximately the same in the control fish throughout the experiment, the concentrations of erythrocytes in the treated fish greatly increased to 1030 × 10^3 μL^{-1} within 24 h of treatment with *C. concavicornis* (Fig. 9). Following this initial sharp increase, the erythrocyte concentrations in the blood slowly decreased to day 10. During the entire 10-d treatment, the circulating erythrocyte concentrations in the treated fish were significantly different from those in the untreated controls at day 1 ($p < 0.05$), day 3 ($p < 0.05$), and day 5 ($p < 0.05$).

Blood Neutrophil Concentrations

The neutrophil concentrations in the blood of both the treated and untreated fish decreased for the first 5 d of the

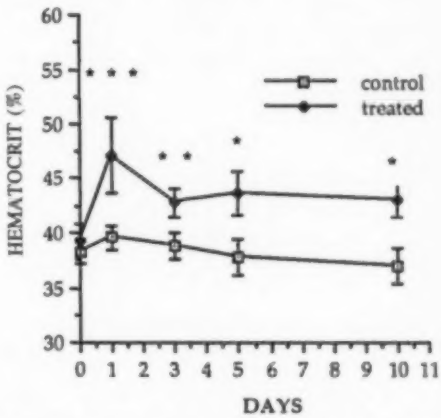

FIG. 8. Mean (of three trials) hematocrit values of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE. *, **, and *** indicate significant differences ($p < 0.05$, $p < 0.01$, and $p < 0.001$), respectively.

experiment. While the neutrophil concentration of the control fish eventually returned to pre-treatment concentrations, the neutrophil concentration in the treated fish remained depressed (Fig. 10). There was a significant difference between the neutrophil concentrations in treated and untreated fish at day 10 ($p < 0.05$).

Blood Lymphocyte Concentrations

The mean concentrations of lymphocytes in blood of the treated and untreated fish immediately prior to *C. concavicornis* treatment were 11.0 × 10^3 and 11.5 × 10^3 μL^{-1}, respectively. During the 10-d experiment, lymphocyte concentrations remained approximately constant in the untreated fish, however, there was an initial (within 24 h) drop in concentration in the treated fish to 4.9 × 10^3 μL^{-1} (Fig. 11). Following this drop, the blood lymphocyte concentrations in the treated fish remained low. The mean lymphocyte concentrations in

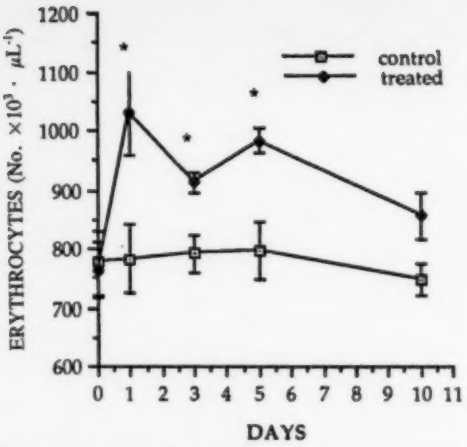

FIG. 9. Mean (of three trials) blood erythrocyte concentrations of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE. and * indicates significant differences ($p < 0.05$).

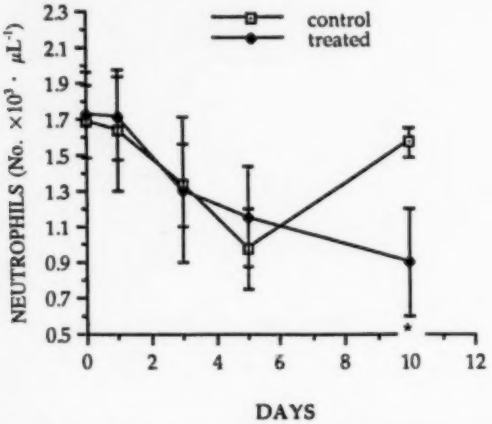

FIG. 10. Mean (of three trials) blood neutrophil concentrations of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE and * indicates significant differences ($p < 0.05$).

the blood of the treated fish were significantly less than those of the control fish at day 1 ($p < 0.05$), day 3 ($p < 0.05$), day 5 ($p < 0.01$), and day 10 ($p < 0.05$).

Blood Thrombocytes

The mean concentrations of thrombocytes in blood of the treated and untreated fish immediately prior to *C. concavicornis* treatment were 11.0×10^3 and 11.9×10^3 μL^{-1}, respectively. Twenty-four hours after treatment, a sharp drop to 4.7×10^3 thrombocyte cells·μL^{-1} occurred. Following this initial drop the thrombocyte concentration continued to gradually decrease with time (Fig. 12). The thrombocyte concentration in the untreated fish showed a slight drop within 24 h; however, during the remainder of the experiment there was a gradual increase in the concentration of these cells. The mean thrombocyte concentrations in the circulating blood of the treated fish were significantly less than those of the

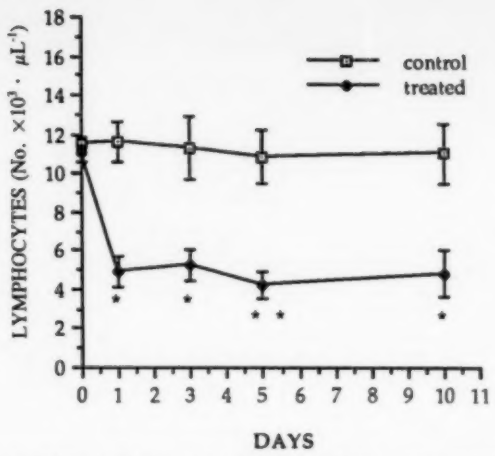

FIG. 11. Mean (of three trials) blood lymphocyte concentrations of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE. * and ** indicate significant differences ($p < 0.05$ and $p < 0.01$), respectively.

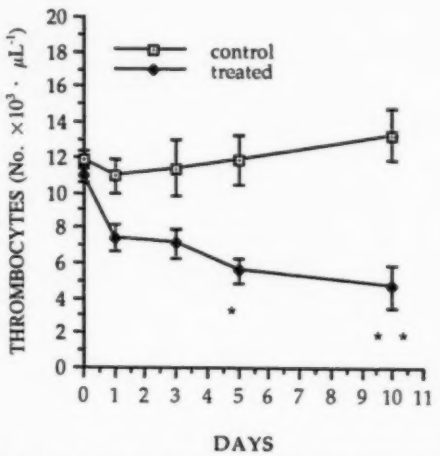

FIG. 12. Mean (of three trials) blood thrombocyte concentrations of chinook salmon exposed (solid triangles) to *C. concavicornis*. Controls are indicated by open squares. Error bars indicate ±SE. * and ** indicate significant differences ($p < 0.05$ and $p < 0.01$), respectively.

control fish at day 5 ($p < 0.05$) and day 10 ($p < 0.01$). In some cases, some of the thrombocytes were observed to aggregate in the blood of treated fish, with the number of thrombocytes per cluster varying from several to 30.

Discussion

The present investigation shows that the treatment of juvenile coho and chinook salmon with *C. concavicornis* under laboratory conditions causes mortality at concentrations as low as 15 cells·mL^{-1} seawater. The cumulative mortality rate of the juvenile coho salmon (Fig. 3) was higher than that of chinook salmon (Fig. 4) when they were exposed to approximately the same concentration of *C. concavicornis*. The causes of fish death appeared to be hypoxia, acid-base

disturbance, and eventually, respiratory failure caused by the accumulation of excessive amounts of mucus on the respiratory epithelium (Yang and Albright 1992). The increased numbers of circulating erythrocytes in treated fish (Fig. 9) support the observation that fish became hypoxic.

In a previous study, Yang and Albright (1992) noted that many cells of *C. concavicornis* became "wedged" in the intersecondary and primary lamellar spaces of rainbow trout upon exposure to this phytoplankter. They also noted that some of the barbed spines had penetrated the lamellar cells. In all cases where the trout were exposed to harmful concentrations of *C. concavicornis*, excessive amounts of mucus accumulated on and between the gill lamellae. In this investigation we observed a similar accumulation of large numbers of *C. concavicornis* cells in the interlamellar spaces of the secondary and primary lamellae of the chinook salmon, along with an accumulation of mucus on the respiratory epithelium (Fig. 5A). Based on these observations, it appears that the responses of the gill tissues of chinook salmon are similar to those of rainbow trout (Yang and Albright 1992).

When the topography of the lamellar surfaces was closely examined, several effects of the harmful *Chaetoceros* were noted. The microridges of the lamellae of untreated chinook salmon were well developed (Fig. 5B). However, following 72-h exposure to *C. concavicornis* the microridges became much less defined (Fig. 5C). In addition to the apparent loss of microridges, we also noted that there were increases in the prominence and apparent numbers of goblet cells per unit area of the respiratory epithelium of the treated chinook salmon (Fig. 5B and 5C). Based on these observations, it would appear that the microridges may become coated and therefore masked by the accumulation of large amounts of mucus produced by the goblet cells that are activated in the presence of harmful concentrations of *C. concavicornis*.

Because microridges are likely used to increase the surface area of the primary lamellae (Hughes 1979; Fishelson 1980), their diminution in the presence of harmful *Chaetoceros* spp. is another factor limiting the exchange of gases and metabolic wastes.

Hyperglycemia is a frequently used indicator of stress in teleost fishes and its magnitude and duration are strongly dependent upon the species and nutritional status of the fish (Nakano and Tomlinson 1967; Wendt and Saunders 1973). There is evidence that catecholamines are directly and cortisol indirectly, involved in regulating the concentration of blood glucose (Klinger et al. 1983). Under hypoxia, lactate is mainly produced through anaerobic muscle metabolism in teleost fish (Joshi 1978). Jorgensen and Mustafa (1980) reported that increased plasma lactate levels were found in different species of teleosts following hypoxia.

The increases we observed in hematocrit values and erythrocyte concentrations in the yearling chinook exposed to *C. concavicornis* (Fig. 8 and 9), have also been observed by other investigators studying the effect of stressors on finfish, including rainbow trout and salmon. Holeton and Randall (1967) observed that hematocrits of rainbow trout increased under hypoxia. Swift and Lloyd (1974) observed an elevation in hematocrits of rainbow trout exposed to crowded conditions and high temperatures. In this latter case, hemoconcentration was attributed to stress, including hypoxia caused by the decrease in oxygen due to high temperature, followed by release of erythrocytes from storage organs. Similarly, McLeay (1975) observed that erythrocyte counts of coho salmon held under crowded conditions and high temperatures were also elevated. Privolnev (1954) and Ostroumova (1964) both found that erythrocytes entered the arterial circulation, likely from the spleen, under the influence of hypoxia. Hall (1928) showed that in several marine fish, asphyxia caused contractions of the spleen.

Based on these earlier observations and our data, it would appear that the increases in hematocrit values and erythrocyte concentrations shown in Figs. 8 and 9 may be mainly due to the entry of erythrocytes into the circulatory system from storage organs, such as the spleen. There may have been some influence of hematopoiesis in the latter part of experiment because increased numbers of reticulocytes were observed when kidney tissue sections were examined. The loss of fluids in the peripheral blood probably also had some influence on increased hematocrits.

The rather mild manipulations of the untreated control fish during these experiments did not affect any of the blood components that were assayed except for neutrophils (Fig. 10). Neutrophil concentrations in the control fish decreased for 5 d after initiation of the experiments. Yet, by day 10, concentrations had returned to pre-trial levels (Fig. 10).

The literature is ambiguous with respect to the influence of stress on the concentration of circulating neutrophils in finfish. Lymphocytopenia and simultaneous neutrophilia was demonstrated by Johansson-Sjobeck et al. (1978) and Ellsaesser and Clem (1986). Pickering (1984) and Pickering and Pottinger (1985) did not find any effect of either transitory or chronic cortisol administration on concentrations of circulating neutrophils in brown trout (*salmo trutta*). However, Wiik et al. (1989) reported that treatment with cortisol for 1 d caused neutropenia. It would appear that in some manner, the neutropenia in the control fish that we observed may be a response to the stress of manipulation during the course of the experiment.

The present study revealed a marked and highly significant suppression of the concentration of circulating lymphocytes and thrombocytes in the fish treated with *C. concavicornis*. This type of lymphocytopenia and thrombocytopenia is a typical response of salmonids to a wide variety of acute and chronic stressors (Pickering et al. 1982; Pickering and Pottinger 1987). Evidence is now accumulating that lymphoid tissue and leucocyte activity in fish are strongly suppressed by corticosteroids (Pickering 1984). Pickering (1986) reported that a marked lymphopenia occurred during sexual maturation in brown trout and that this was closely correlated with elevated plasma cortisol levels. Ellsaesser and Clem (1986) have demonstrated that both the number and the immunological competence of circulating lymphocytes in the blood of channel catfish (*Ictalurus punctatus*) were reduced during stress.

Wiik et al. (1989) have shown that cortisol treatment caused a reduction in circulating lymphocytes and thrombocytes. Klinger et al. (1983) observed a decrease in plasma thrombocyte concentrations with increased stocking density of channel catfish. Pickering and Pottinger (1987) showed that chronic crowding stress caused a marked and prolonged reduction in the circulating thrombocytes of both brown and rainbow trout. Pickering and Pottinger (1988) also showed that a marked lymphopenia and thrombopenia occurred in Atlantic salmon (*Salmo salar*) S_2 parr that had chronically elevated blood cortisol levels during the winter

months. Wiik et al. (1989) observed that in Atlantic salmon treated with cortisol for 4 d, the thrombocytes became aggregated. They suggested that clustering was an effect of cortisol administration. They found that the fish that showed the clustering phenomenon were very susceptible to cold-water vibriosis. We have also noted that fish that had aggregated thrombocytes were more susceptible to vibriosis than untreated control fish (unpublished observations).

Neutrophils, lymphocytes, and thrombocytes of salmonids are significant components of the immune system (Anderson 1974; Corbel 1975; Post 1978). Because of this, a depletion of the quality and quantity of these cells would influence their ability to either become or remain immunocompetent. In this connection, the earlier observations of Albright et al. (1993) are significant. When the water in which coho salmon were held was treated with approximately 50 cells·mL^{-1} of *C. concavicornis* and 2×10^6 cells·mL^{-1} of *Vibrio anguillarum* all of the fish died of vibriosis within 4 d of what would otherwise have been a nonlethal exposure to this bacterium. The data reported here suggest that this may be, at least in part, due to suppression of the neutrophil, lymphocyte, and thrombocyte component of the immune system of chinook salmon.

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Variability in First-Year Growth of Yellow Perch (*Perca flavescens*): Predictions from a Simple Model, Observations, and an Experiment

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Post, J.R., and D.J. McQueen. 1994. Variability in first-year growth of yellow perch (*Perca flavescens*): predictions from a simple model, observations, and an experiment. Can. J. Fish. Aquat. Sci. 51: 2501–2512.

First-year growth of yellow perch, *Perca flavescens*, varies by greater than an order of magnitude among populations and among cohorts within populations. The variability in growth rates of natural and enclosure-reared young-of-the-year yellow perch could be explained by the availability of benthic and/or planktonic prey (R^2 = 0.093–0.098). Mean annual water temperature and cumulative degree-days did not add to the explanatory power of the relationships. The faster growing natural cohorts included more benthos in their diet; however, benthos is not necessary to sustain the highest growth rates because the fastest growth rates were observed in enclosure cohorts that lacked benthic invertebrates. Cohorts in lakes and enclosures that had a high proportion of *Daphnia* in the zooplankton community also supported higher first-year growth rates. The results of the enclosure experiment suggest that the dominant mechanism creating growth variability is density-dependent intra-age-class competition. Our empirical results, when coupled with a simple model, suggest that the assumption of a negative relationship between energetic costs of foraging and prey abundance, on a daily time scale, is the most appropriate because it acts to amplify growth variability across ranges of prey abundance.

La croissance de la perche, *Perca flavescens*, au cours de sa première année de vie, varie de plus d'un ordre de grandeur à l'intérieur des populations et à l'intérieur des cohortes dans les populations. La variabilité des taux de croissance des perches de l'année élevées en milieu naturel et en enclos peut s'expliquer par la présence de proies benthiques ou planctoniques (R^2 = 0,093–0,098). La température annuelle moyenne de l'eau et les degrés-jours cumulés n'ont pas fourni d'explication additionnelle. Le régime alimentaire des cohortes naturelles dont la croissance était plus rapide comprenait plus d'éléments benthiques, mais ces derniers ne sont pas nécessaires pour soutenir les taux les plus élevés de croissance, puisque la croissance la plus rapide a été observée chez les cohortes vivant dans des enclos dépourvus d'invertébrés benthiques. Les cohortes des lacs et des enclos dans lesquels la communauté planctonique comprenait une proportion élevée de *Daphnia* ont également montré un taux de croissance plus élevé au cours de la première année de vie. Les résultats obtenus dans les enclos indiquent que le mécanisme dominant à l'origine de la variabilité de la croissance est une concurrence dépendante de la densité qui survient à l'intérieur des classes d'âge. Nos résultats empiriques, une fois couplés à un modèle simple, laissent croire que l'hypothèse d'une relation négative entre le coût énergétique de la recherche de nourriture et l'abondance des proies, à l'échelle quotidienne, soit la plus appropriée, car elle amplifie la variabilité de la croissance dans toute la gamme d'abondance des proies.

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Growth is the product of a complex of physiological, ecological, and physical processes. Physiological processes that affect growth include standard and active metabolism, consumption, energetic costs of acquiring and processing food, egestion, and excretion. Ecological processes include predator–prey functional responses and the energetic costs of interference competition and of other behaviours. Physical processes include temperature- and light-dependent processes and physical habitat complexity. Understanding growth patterns in nature is difficult because most of these physiological, ecological, and physical processes interact, often in nonlinear ways. It is primarily for this reason that laboratory experiments involving growth generally ensure that all factors but one have been held constant and a single variable manipulated. Such laboratory experiments have documented the effects of these processes on whole-organism energetics and growth (see reviews by Brett and Groves 1979; Brett 1979; Tytler and Calow 1985; Wootton 1990). On the other hand, results from field studies concerning energetics and growth have been less clear cut. Sometimes energy budgets balance reasonably (Rice and Cochran 1984; Beauchamp et al. 1989; Fox 1991), other times not (Boisclair and Leggett 1989a, 1989b, 1989c; Post 1990). If a reasonable balance is achieved in this energy budgeting exercise, authors usually suggest that their budgets must incorporate the critical processes both quantitatively

TABLE 1. Location, morphometry, and fish communities of the study lakes. The dominant fish species during the years of study are listed in rank order: Yellow perch (Yp), golden shiner (Gs), pumpkinseed (Ps), bluegill (Bg), cyprinids (Cy), *Micropterus* (Mi).

Lake	Location		Area (ha)	Depth (m)		Fish community
	Longitude	Latitude		Mean	Maximum	
St. George	43°57′N	79°25′W	10.4	5.7	15.0	Yp, Gs, Ps
Eaton	43°57′N	79°31′W	10.9	5.8	15.0	Bg, Yp
Harp	45°23′N	79°08′W	66.9	12.4	40.0	Yp, Cy, Mi
Dickie	45°09′N	79°05′W	93.2	5.0	12.0	Yp, Mi
Clear	45°12′N	78°43′W	96.0	12.4	33.0	Cy, Yp

and qualitatively. If not, authors typically suggest that there are either quantitative or qualitative errors in one or more bioenergetic functions or that critical bioenergetic functions are completely missing. Literature reports rarely recognize that there are other explanations than those used, whether budgets balance or not. This must be acknowledged explicitly and leads us to suggest that energy budgeting cannot be used as a confirmatory tool to explain hypotheses about what controls (or alternatively does not control) growth in nature.

We propose instead a testable hypothesis that is based on the simple but eloquent ideas of the predator–prey functional response (Holling 1965) and optimal foraging theory (Kerr 1971a, 1971b; Werner and Hall 1974). Clearly if prey are unavailable, consumption must be zero and growth negative (to pay off metabolic costs). If prey are abundant, predators will satiate and there will be an upper bound to rates of consumption (based on various time constraints) and, therefore, an upper bound to growth. Therefore, we propose that the most parsimonious hypothesis to test is that growth is simply a function of prey availability.

To address this hypothesis, we chose young-of-the-year (YOY) yellow perch, *Perca flavescens*. YOY fish were selected because they provide the most sensitive test, as small fish have the greatest scope for growth and hence the greatest potential for variability in growth. YOY cohorts also start out at the same size, thus avoiding the problems of using older fish for which initial sizes vary substantially creating allometric effects that complicate analyses (see comments and rebuttals by Hayward 1990; Boisclair and Leggett 1990; Hewett et al. 1991; Boisclair and Leggett 1991).

We tested this hypothesis over single growing seasons because (1) body sizes and growth rates of yellow perch during the first year of life have been identified as critical in modifying mortality and recruitment in YOY fish (Post and Prankevicius 1987; Miller et al. 1988; Post and Evans 1989a, 1989b; Post and Rudstam 1992) and (2) other interesting studies aimed at addressing questions of variability in growth rates have operated at the same time scale (Boisclair and Leggett 1989a, 1989b, 1989c; Fox 1989; Fox and Flowers 1990).

There are four components to this research. First, a simple model was developed that makes qualitative predictions of the interactions among prey abundance, foraging energetics, interference competition energetics, consumption rates, and growth rates. Second, the literature was surveyed to describe the magnitude of variability in growth of YOY yellow perch. Third, growth trajectories and prey biomass were assessed for eight natural cohorts of YOY yellow perch in five lakes. And fourth, an in situ enclosure experiment was performed in which prey availability was manipulated by varying stocking density of YOY yellow perch and measuring growth trajectories and prey abundance for six cohorts.

Materials and Methods

Natural Lakes

The growth rates of YOY yellow perch were measured for the 1982, 1984, and 1985 cohorts in Lake St. George and for the 1985 cohorts in Eaton, Dickie, Harp, and Clear lakes (Table 1). All lakes are in Ontario. YOY yellow perch were captured at weekly to monthly intervals for each of the cohorts. During the pelagic phase, sampling was conducted with a Miller sampler in 1982 (see Post and McQueen (1988) and Post (1990) for sampling design), and in 1984 and 1985 using a fine mesh (1 × 1 mm) purse seine (30 m long, 9 m deep) similar in design to that described by Evans and Johannes (1988). Once the YOY yellow perch migrated to the littoral zone, they were captured with a fine-mesh (1 × 1 mm) beach seine (30 m long, 1.6 m deep). A minimum of four purse seine and four seine sites were sampled on each sampling date for each lake. If necessary, additional sites were sampled until a minimum of 50 YOY yellow perch were captured. All YOY yellow perch captured in 1982 in Lake St. George were preserved in 70% ethanol and subsequently measured (total length) to the nearest 1 mm and weighed (preserved weight) to the nearest 0.01 g. Fresh length and weight were calculated from preserved weight using empirically determined preserved–fresh relationships for length and weight. All YOY yellow perch captured in 1984 and 1985 were measured fresh for total length to the nearest 1 mm and weighed wet to the nearest 0.01 g and frozen for subsequent stomach analysis. In the laboratory a random subsample of 10 fish per lake per date was selected from the sample site with the greatest abundance of YOY yellow perch and their stomach contents removed and pooled for a diet description.

Pelagic zooplankton in Lake St. George was sampled weekly at the central station with a 35-L Schindler trap at six to eight discrete depths and subsamples combined to characterize the whole water column (see McQueen et al. (1989) for additional details of sampling and subsampling). In Eaton, Clear, Dickie, and Harp lakes pelagic zooplankton was sampled with a 47-cm-diameter, 150-μm-mesh vertical haul net at the central station of each lake on the same dates as the fish were collected. Sampling depth was 10 m in

Dickie Lake and 12 m in Eaton, Harp, and Clear lakes. Littoral zooplankton was sampled with a 35-L Schindler trap at approximately 1.5 m depth at each of the beach seine sites. One 10-mL random subsample was taken from each littoral sample that previously had been diluted to 100 mL and were pooled, creating a single sample representing littoral zooplankton. A random subsample of 300–500 zooplankton from each pelagic and littoral sample was identified, counted, and measured using a computer-assisted caliper system (Sprules et al. 1981; Post 1984) and biomass was calculated using genus-specific length–weight regressions (Post 1984).

Benthic invertebrate samples were collected using an Eckman Grab (15.5 cm^3) in the littoral zones of all lakes except Eaton Lake (St. George 1982: 3 visits, 18 samples; St. George 1984: 4 visits, 30 samples; St. George 1985: 4 visits, 30 samples; Dickie: 6 visits, 93 samples; Harp: 6 visits, 140 samples; Clear: 5 visits, 79 samples). Invertebrates were sorted from the sediments by eye within 24 h of collection and preserved in 70% ethanol. In the laboratory, the invertebrates were identified to order and weighed to the nearest 0.1 mg wet weight (Lake St. George) and 0.01 mg dry weight (Clear, Dickie, and Harp lakes). Benthic biomass was calculated on a wet weight aerial basis assuming a 10:1 wet–dry weight ratio.

The zooplankton in the stomach-content samples were analyzed in the same manner as were the lake zooplankton samples. All benthic invertebrates found in stomach samples were identified to order, counted, and weighed (wet weight). Fish prey were counted and weighed. The relative proportion of zooplankton, benthos, and fish in the diet on a wet weight basis was calculated.

Temperature was measured at 1-m depth intervals at the central station of each lake and a mean epilimnetic temperature calculated for the dates when the YOY yellow perch were abundant in the open water. Once the fish migrated to the littoral zone and were caught in beach seines, temperature was measured at 0.5 m depth at each beach seine site and averaged among sites to determine a mean littoral zone temperature. Cumulative degree-days and mean seasonal temperatures were calculated assuming a linear change in temperature between empirical measurements.

Experimental in situ Enclosures

The enclosure experiments were conducted in the pelagic zone of Lake St. George in 1982 (two enclosures) and 1985 (four enclosures). The enclosures were 8 m in diameter and 16 m deep, and constructed of an impermeable polyvinyl covered nylon tube with the bottom buried in the sediment. Details of the construction, fertilization, and experimental protocol are available in Post and McQueen (1987). YOY yellow perch were captured in Lake St. George by purse seine and beach seine and stocked into the enclosures at a range of densities in June of both years. YOY yellow perch that were used for estimating growth rates, were captured bimonthly to monthly in the enclosures using Plexiglas fish traps (51 × 38 × 38 cm) (Casselman and Harvey 1973), Gee minnow traps (40 × 25 cm), and Windermere traps (90 × 57 cm) in 1982 and with the same purse seine used in the lakes in 1985. All captured fish were measured (total length) to the nearest 1 mm, weighed wet to the nearest 0.01 g, and returned live to the enclosures.

Zooplankton were sampled weekly using a 47-cm vertical haul net from 12 m depth in each enclosure and were enumerated using the same protocol as was used for the pelagic lake samples. Weekly temperature profiles were taken at 1-m intervals in the enclosures and mean epilimnetic temperatures were calculated. In September and October, Schnabel multiple census mark–recapture experiments (Schnabel 1938) were conducted in each enclosure using the gear described to estimate the density of YOY yellow perch.

Data Analysis

Mean daily growth rates were calculated for each natural and enclosure cohort by summing the first and last mean weight estimate and dividing by the number of days between the estimates. Mean zooplankton biomass, benthos biomass, proportion of *Daphnia* by weight in the total zooplankton biomass, and mean temperature are arithmetic means of all of the data collected from June to October for each cohort.

Results

Conceptual Model

Growth represents the energy remaining after various metabolic costs and waste losses are removed from consumed energy where

(1) Growth = consumption − (metabolic costs + waste costs).

Energy consumed is typically a function of prey abundance and can be characterized as a type II functional response (Holling 1965) where

$$(2)\quad \text{Consumption} = \frac{aTN}{1 + ahN}$$

where a is the rate of effective search, T is the total time available for foraging, N is the density of prey, and h is the handling time per prey item. We assume that handling time is primarily digestion time because it is much longer than the time required for prey attack, manipulation, and ingestion, following the arguments of Breck (1993). The functional forms of this relationship is that of an asymptotic curve with the slope approaching zero at high prey density.

Total metabolic costs include standard metabolism, specific dynamic action plus the costs of foraging activity and other activities such as interference competition where

(3) Metabolic costs = standard metabolism
+ specific dynamic action
+ foraging costs
+ interference costs
+ other activity costs.

The energetic cost of foraging has been implicated as critical to our understanding of growth variability (Boisclair and Leggett 1989d). Assuming that the energetic cost of foraging is directly proportional to the time spent foraging, then

$$(4)\quad \text{Foraging cost} \propto T - h\,(\text{consumption}) \propto T - h\left(\frac{aTN}{1 + ahN}\right).$$

This relationship implies that predators divide their time between foraging, which has an energy cost above standard metabolic rate, and digestion, which has an energy cost representing apparent heat increment plus standard metabolic rate. Therefore, foraging incurs an energetic cost that is

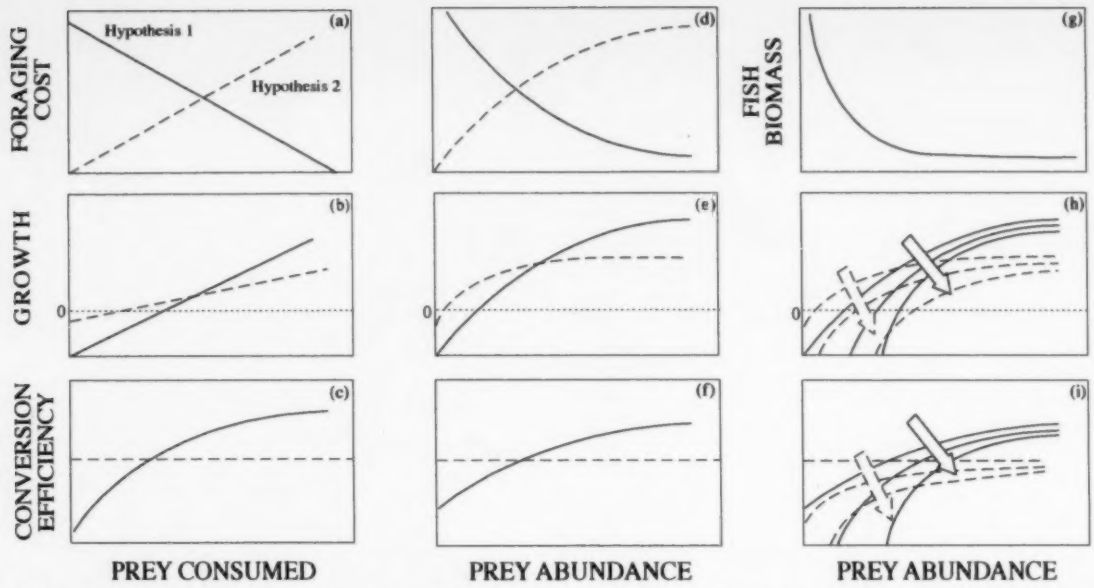

FIG. 1. Foraging cost, growth efficiency, and conversion efficiency as a function of prey consumed (a, b, and c) and prey abundance (d, e, and f) as predicted by a simple model based on the type-2 functional response. The empirical relationship between prey abundance and fish biomass (zooplankton and zooplanktivore) determined by McQueen et al. (1986) (g) and the relationship between growth (h) and conversion efficiency (i) versus prey abundance with varying levels of interference competition costs proportional to fish biomass are shown. The arrows indicate the direction of the effect of increasing levels of interference competition. Solid lines and arrows and broken lines and arrows refer to foraging hypotheses 1 and 2, respectively.

directly proportional to time spent foraging and handling cost is independent of time spent foraging. As a function of prey consumed, this foraging cost hypothesis (referred to hereafter as hypothesis 1) produces a negative linear relationship (Fig. 1a). As a function of prey abundance, this hypothesis implies a negative exponential relationship (Fig. 1d).

A second foraging cost hypothesis has been proposed by Kerr (1982) and accepted by Boisclair and Leggett (1989d). They hypothesize that foraging costs are positively and linearly related to consumption (hereafter referred to as hypothesis 2) (Fig. 1a). As a function of prey abundance, hypothesis 2 implies a positive curvilinear relationship increasing to an asymptote (Fig. 1d).

Therefore, we can calculate growth using Equations (1) and (3) for the two foraging cost hypotheses:

(5) Hypothesis 1

$$\text{Growth} \propto \frac{aTN}{1 + ahN} - T - h\left(\frac{aTN}{1 + ahN}\right)$$

(6) Hypothesis 2

$$\text{Growth} \propto \frac{aTN}{1 + ahN} - C\left(\frac{aTN}{1 + ahN}\right)$$

where C is a constant energy cost per prey item.

These alternate models are presented as conceptualizations of bioenergetic processes rather than complete and balanced budgets. We now use these models to qualitatively assess the implication of alternative foraging cost hypotheses on growth and conversion efficiencies of fish.

Both foraging hypotheses produce positive linear relationships between prey consumed and growth with a greater slope for hypothesis 1 (Fig. 1b). Both foraging hypotheses produce asymptotic relationships with higher asymptotic growth rate and a lower growth rate at low prey abundance for hypothesis 1 (Fig. 1e). The two foraging cost hypotheses imply different relationships between conversion efficiency and prey consumed and prey abundance. Hypothesis 1 implies a nonlinear positive asymptotic relationship between conversion efficiency and both prey consumed and prey abundance (Fig. 1c and 1f). Hypothesis 2 implies a constant conversion efficiency as a function of both prey consumption and prey abundance (Fig. 1c and 1f).

The energetic cost of interference amongst individuals has also been proposed as potentially important in modifying growth (Boisclair and Leggett 1989d). We assume for simplicity that prey abundance is negatively related to fish biomass, in the form demonstrated empirically by McQueen et al. (1986):

(7) $\log(\text{fish biomass}) = a + b \log(\text{prey abundance})$

where a and b are regression coefficients (Fig. 1g). McQueen et al. (1986) manipulated biomass in enclosures by stocking a range of fish densities. We assume here that increases in fish biomass are directly related to fish density. We also assume that the energetic costs of interference interactions are positively and linearly related to fish biomass following the assumption that the frequency of encounters is density-dependent. Using Equations (1) and (3) we can examine the impact of interference costs on growth and conversion efficiency as a function of fish biomass. Of course, these calculations assume that there is an energetic cost of interactions amongst individuals. This may or may not be applicable to the shoaling species for which Equation (7) was developed by McQueen et al. (1986). The effect of this hypothesized

TABLE 2. Literature review of mean sizes and variability in mean size of YOY *Perca* spp. among years in lakes and among lakes. Lake location, sample size (N), mean size (in total length or in wet weight), standard deviation (SD), coefficient of variation (CV), and range in sizes are reported.

Species	Lake	N	Mean	SD	(CV)	Range	Units	Reference(s)
P. flavescens	Red Lakes, USA	20 yr	69.4	9.1	(13)	54–88	mm TL	Pycha and Smith 1955; Ney and Smith 1975
P. fluviatilis	Mozhaisky Reservoir, Russia	8 yr	62.0	8.38	(14)	52–77	mm	Spanovskaya and Grygorash 1977
P. fluviatilis	Mozhaisky Reservoir, Russia	8 yr	4.18	2.07	(50)	8.4–20.5	g wet	Spanovskaya and Grygorash 1977
P. flavescens	Ferguson Reservoir, USA	6 yr	126.0	16.5	(13)	117–159	mm TL	Paxton and Stevenson 1978
P. flavescens	Killdeer Reservoir, USA	4 yr	116.5	5.0	(4)	110–122	mm TL	Paxton and Stevenson 1978
P. flavescens	Winnebago, USA	5 yr	85.0	4.3	(5)	81–91	mm TL	Weber and Les 1982
P. flavescens	Winnebago, USA	5 yr	6.7	0.67	(10)	5.8–7.5	g wet	Weber and Les 1982
P. flavescens	Oneida, USA	12 yr	68.8	7.8	(11)	58–86	mm TL	Nielsen 1980
P. flavescens	Oneida, USA	11 yr	4.0	1.25	(35)	0.66–2.27	g wet	Mills et al. 1989
P. flavescens	Various, North America[a]	8 lakes	68.4	11.9	(17)	48–86	mm TL	Review by Keast 1977
P. fluviatilis	Various, Europe[b]	3 lakes	71.7	10.4	(15)	60–80	mm TL	Review by Persson 1983
P. flavescens	Various, Ontario	8 lakes	61.4	6.0	(10)	55–72	mm TL	This study
P. flavescens	Various, Ontario	8 lakes	2.00	0.52	(26)	1.39–2.88	g wet	This study
P. flavescens	St. George, Ontario	3 yr	63.9	7.7	(12)	56–72	mm TL	This study
P. flavescens	St. George, Ontario	3 yr	2.34	0.53	(22)	1.83–2.88	g wet	This study
P. flavescens	Enclosures: St. George	6	63.9	7.7	(12)	47–104	mm TL	This study
P. flavescens	Enclosures: St. George	6	2.34	0.53	(22)	0.94–9.61	g wet	This study

[a]Only data for single lakes were included in the summary.
[b]Only single European lakes were included in the summary.

interference cost to growth rates and conversion efficiency is most pronounced at low prey abundance and minimal at high prey abundance (Fig. 1h and 1i). The slope of the relationship with prey abundance increases for foraging hypothesis 1 and changes from a slope of zero to a positive slope for foraging hypothesis 2.

Observations and Experiments

Substantial interannual and interlake variability in the first-year growth of yellow perch appears to be the norm (Table 2). The maximum range in fall mean length across lakes and years reported in the literature is 48–159 mm total length. Assuming isometric growth, this length range translates into a weight range across years and lakes of approximately 36 times.

The eight natural cohorts of YOY yellow perch for which we measured growth, varied in fall mean total length from 55 to 72 mm and in mean weight from 1.4 to 2.9 g (Fig. 2 and 3; Table 3). The six cohorts raised in pelagic enclosures in Lake St. George varied in fall mean total length from 47 to 103 mm and in mean weight from 0.9 to 9.7 g (Fig. 2 and 3; Table 3).

The observed variability in growth amongst the natural cohorts was explained poorly by the availability of either zooplankton or benthic prey (Fig. 4) ($R^2 = 0.08$, $N = 8$; $R^2 = 0.33$, $N = 7$, respectively) separately. A combined model of zooplankton and benthos biomass explained a significant proportion of the variability in growth of YOY yellow perch (Fig. 5) ($R^2 = 0.98$, $N = 7$, $p < 0.05$). The data were best fit with a linear relationship; all higher order interactions were nonsignificant ($p > 0.05$). The addition of mean epilimnetic temperature or cumulative degree-days to the regression analysis did not add significantly to the explanatory power of the relationship ($p > 0.05$). The use of zooplankton and benthic prey by YOY yellow perch varied amongst cohorts (Fig. 6). All cohorts included some benthos in their diet, ranging from a minimum contribution of 1% by weight for the Lake St. George 1984 offshore cohort to a maximum contribution of 94% for the Eaton Lake 1985 cohort. The Lake St. George 1982 cohort, which had the fastest growth rates early in the season, also included a substantial component of larval fish in their diet (Fig. 6).

In the enclosure experiment, zooplankton biomass explained a significant proportion of the observed variability in growth rates (Fig. 7) ($R^2 = 0.93$, $N = 6$, $p < 0.05$). This is consistent with the observation from a literature survey, that the maximum sizes of YOY yellow perch in the Lake St. George enclosures approached the largest sizes observed for the species (Table 2). The addition of mean epilimnetic temperature or cumulative degree-days to the regression analysis did not add significantly to the explanatory power of the relationship ($p > 0.05$).

The prey biomass versus growth rate relationships were different for the cohorts from natural lakes and the cohorts in experimental enclosures (Fig. 4, 5, and 7). Examination of the difference in prediction between the two models shows that, at low zooplankton biomass, lake fish have higher growth rates than enclosure fish and, at high zooplankton biomass, the enclosure fish have higher growth rates than lake fish (Fig. 8). The growth-rate differences at low zooplankton biomass can be readily explained because the lake fish also use benthic invertebrates that are unavailable to fish in the pelagic enclosures. The two cohorts with large positive growth differences (Fig. 8) are Eaton 1985 and Clear 1985, both of which have low zooplankton biomass and a substantial proportion of benthos in their diet (Fig. 6). On

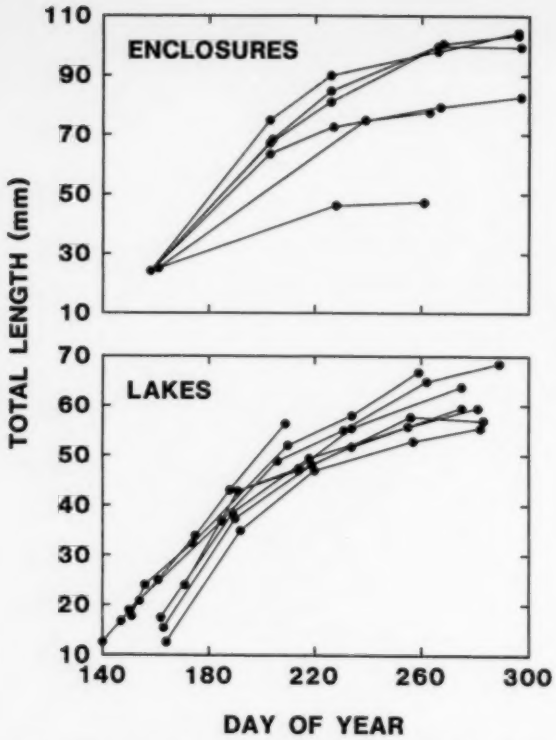

FIG. 2. Growth in total length of YOY yellow perch in enclosures and lakes. Points are mean total lengths based on sample sizes of 10–334 fish. Total sample sizes for each lake and enclosure are quoted in Table 2. Note the difference in scale on the *y* axes of the growth curves for fish in enclosures and lakes.

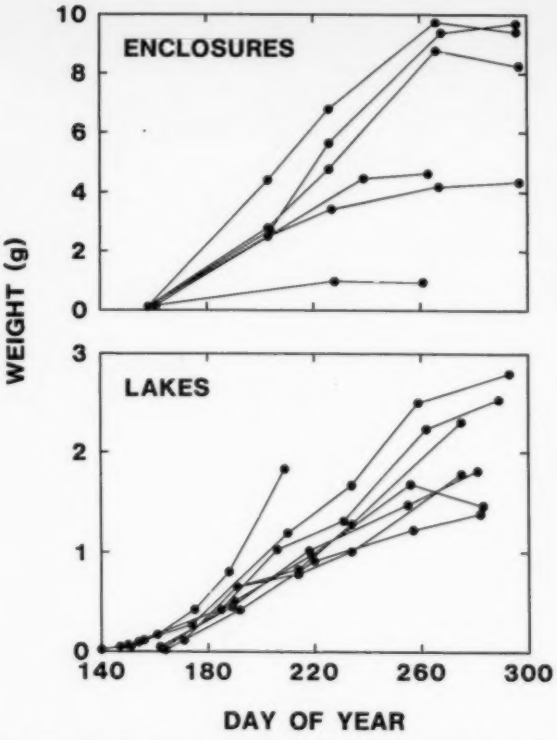

FIG. 3. Growth in wet weight of YOY yellow perch in enclosures and lakes. Points are mean wet weights based on sample sizes of 10–334. Total sample sizes for each lake and enclosure are quoted in Table 2. Note the difference in scale on the *y* axes of the growth curves for fish in enclosures and lakes.

the other hand, lower growth rates in lakes than in enclosures at the same zooplankton biomass is more difficult to understand. The explanation may involve the taxonomic composition of the zooplankton community. Mills and Forney (1981) demonstrated that high growth rates of YOY yellow perch were sustained only in years when *Daphnia* were a large component of the zooplankton community. In our study, growth rates greater than approximately 0.02 $g \cdot d^{-1}$ were sustained only when the proportion of *Daphnia* in the zooplankton community exceeded approximately 20% by weight (Fig. 9). Six of the seven lake cohorts had a proportion of *Daphnia* <15% and, therefore, lower growth rates than enclosure fish with equivalent zooplankton biomass. After an initial pelagic-zone residence, the YOY yellow perch migrate to the littoral zone where *Daphnia* typically make up a small proportion of the total zooplankton biomass. The experimental enclosures were pelagic and sustained a typically pelagic community structure with a substantial proportion of *Daphnia* in the zooplankton community. One lake and one enclosure had a proportion of *Daphnia* atypical of their respective habitats. Lake St. George 1982 had a zooplankton community with 34% *Daphnia* by weight. The lake had recently experienced a winter kill that eliminated 75% of the zooplanktivorous fish and, therefore, a release of predation pressure on *Daphnia* (McQueen et al. 1989). One of the experimental enclosures had a proportion of *Daphnia* of only 12% and a growth rate more typical of lake growth rates. That enclosure had the highest stocking density of YOY yellow perch that preferentially reduced the *Daphnia* abundance producing a community dominated by small-bodied zooplankton (Post and McQueen 1987).

The range in zooplankton biomass among the experimental enclosures was produced by stocking them with a range of densities of YOY yellow perch. Therefore, it might be argued that the observed decline in growth rates at lower zooplankton biomasses is caused by increased energetic costs of interference competition rather than increased foraging costs per prey item. This alternate hypothesis is weakly supported because fish density explained 25% of the unexplained 7% of the variation in the growth versus zooplankton relationship (Fig. 10).

Discussion

It is clear from this study that there is substantial variation in first-year growth of yellow perch, both among cohorts within populations and among populations. Our enclosure experiment demonstrates that the range of growth rates observed in natural cohorts, among populations that differ in their physical and chemical environment and in genotype, can be observed in a single genotype in a single environment. Therefore, in the discussion that follows, we will not consider further the potential influences of physical (except temperature) and chemical environment and of genotype on growth.

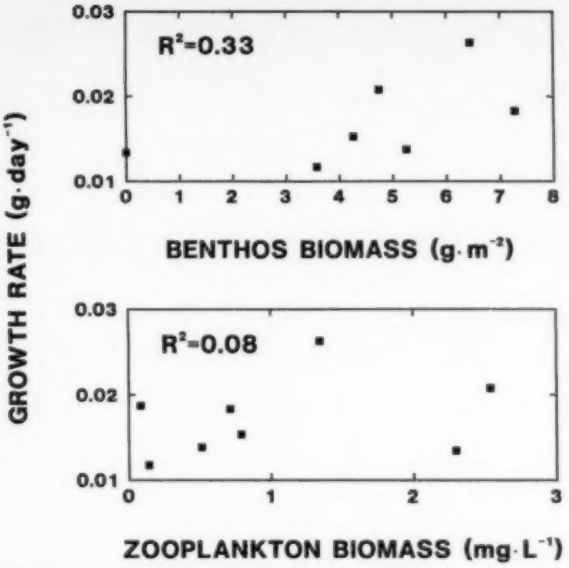

FIG. 4. The relationship of mean daily growth rates of YOY yellow perch in lakes versus mean seasonal benthic invertebrate biomass and mean seasonal zooplankton biomass.

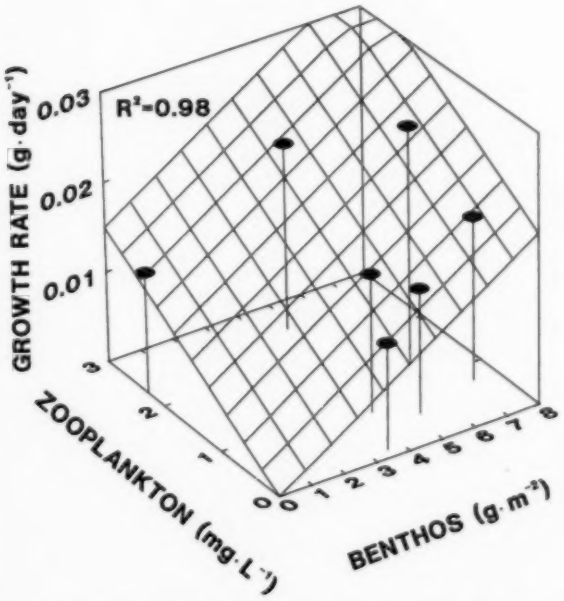

FIG. 5. The relationship of mean daily growth rates of YOY yellow perch in lakes versus mean seasonal zooplankton and benthic invertebrate biomass. The multiple regression relationship is Growth = 0.0050(zooplankton) + 0.00237(benthos).

We, of course, recognize that, at their extremes, the physical and chemical environment and genotype can dramatically influence the potential for growth (see review in Wootton 1990). Empirically, first-year growth of yellow perch was strongly related to the availability of prey for both natural lake cohorts and experimental cohorts in enclosures. Indices of temperature did not add to the explanatory

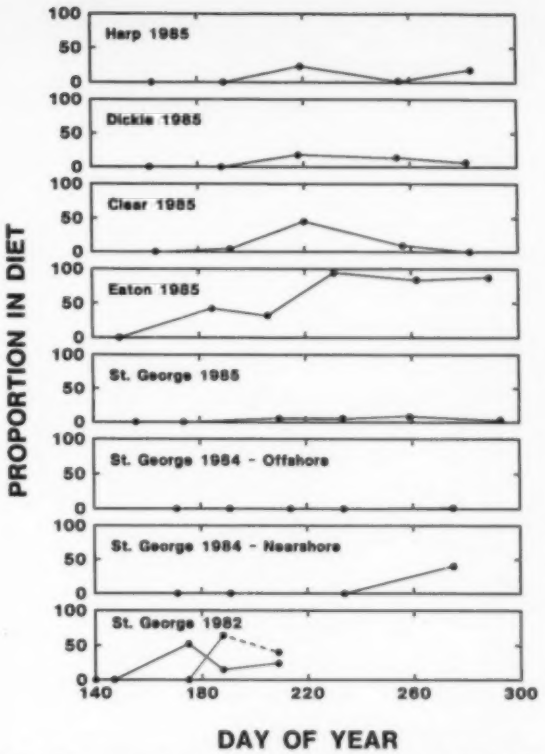

FIG. 6. The proportion of benthos (solid lines) and larval fish (broken line) by biomass in the diet of yellow perch in the eight cohorts in lakes. The remaining proportion of the diet is zooplankton.

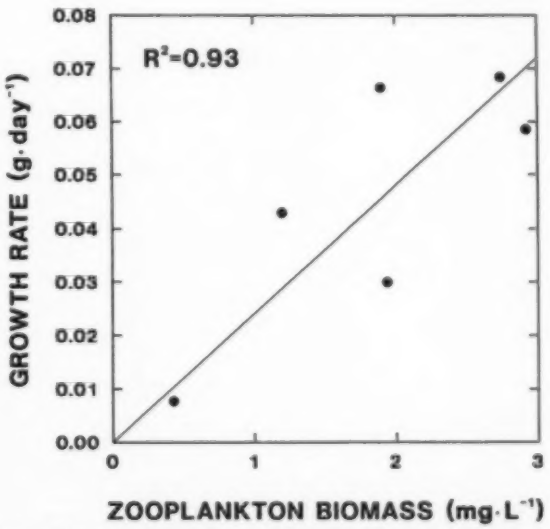

FIG. 7. The relationship of mean daily growth rates of YOY yellow perch in enclosures versus mean seasonal zooplankton biomass. The regression equation is Growth = 0.024(zooplankton).

power of these empirical relationships although it is recognized that the variability in temperature experience of the cohorts was relatively small. A regression analysis of growth

TABLE 3. Mean seasonal growth, size, prey biomass, and percent *Dapnia* data for eight natural lake cohorts and six enclosure cohorts of YOY yellow perch. Sample size is the total number of YOY yellow perch measured for that cohort. Growth rates are means calculated from the pelagic larval phase in spring (May–June) to autumn (September–October) and final mean total length (TL) and wet weight are autumn (September or October) measurements with the exception of the Lake St. George 1982 cohort, for which final measurements were made in August. The Lake St. George 1984 cohort is divided into nearshore (NS) and offshore (OS) cohorts. Mean temperature, range in temperature, and cumulative degree-days between the first and last sampling days are reported. NB = no benthos available for pelagic YOY yellow perch in lakes or enclosures; NA = data not available

Cohort	Sample size	Growth ($g \cdot d^{-1}$)	Final TL (mm)	Mean weight (g)	Benthos ($g \cdot m^{-2}$)	Zooplankton ($mg \cdot L^{-1}$)	Percent *Dapnia*	Temperature (°C)		Cumulative degree-days (°C·d)
								Mean	Range	
					Lakes					
St. George 1982	420	0.026	56.3	1.83	6.45	1.346	34	21.1	16.6–26.1	1456
St. George 1984 NS	340	0.018	63.8	2.30	7.27	0.713	0	22.4	16.5–26.1	2352
St. George 1984 OS	327	0.013	59.4	1.78	NB	2.296	13	21.3	14.5–25.0	2237
St George 1985	828	0.021	71.6	2.88	4.74	2.536	2	20.8	13.0–24.2	2971
Eaton 1985	222	0.019	68.5	2.53	NA	0.084	0	22.1	13.3–25.6	3089
Dickie 1985	524	0.014	59.4	1.81	5.25	0.513	9	21.1	14.1–24.4	2530
Harp 1985	535	0.015	56.9	1.47	4.26	0.791	0	20.9	14.4–24.6	2523
Clear 1985	546	0.012	55.4	1.39	3.57	0.139	0	20.4	15.3–23.1	2424
					Enclosures					
Enclosure A 1982	192	0.008	47.2	0.94	NB	0.430	5	18.9	14.9–22.2	1948
B 1982	97	0.043	77.5	4.63	NB	1.200	76	18.9	14.9–22.2	1948
Enclosure A 1985	176	0.060	99.5	8.25	NB	2.920	82	18.9	11.9–22.4	2630
B 1985	185	0.066	104.4	9.41	NB	1.900	86	18.9	11.9–22.4	2630
C 1985	307	0.300	82.7	4.34	NB	1.940	72	18.9	11.9–22.4	2630
D 1985	179	0.068	103.4	9.69	NB	2.740	85	18.9	11.9–22.4	2630

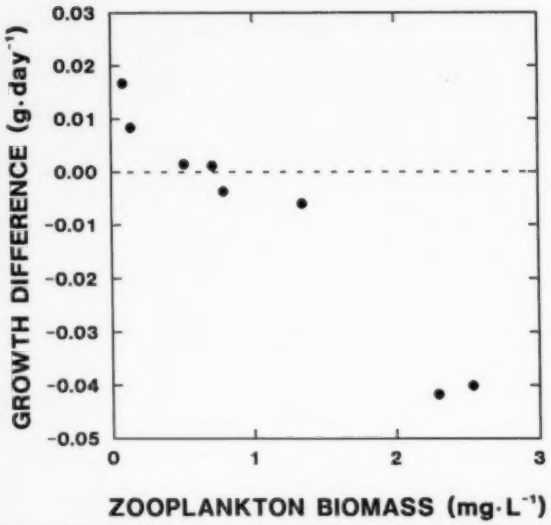

FIG. 8. The difference in mean daily growth rate of YOY yellow perch between that observed in natural cohorts in lakes and that predicted by the growth versus zooplankton biomass regression derived from the enclosure experiments as a function of zooplankton biomass.

rates, prey abundance, and temperature using seasonal means implies that body size, temperature, and consumption are linear processes. Because they are clearly not linear processes, prey availability can affect growth rates differentially for fish that differ in body size and/or ambient temperature exposure (Hewett et al. 1991). With these cautions in mind, we choose to focus on seasonal mean temperatures because, over wide ranges (an order of magnitude or more), seasonal means often explain a substantial portion of the variance in relationships between adjacent trophic levels (McQueen et al. 1986). A strong relationship between seasonally averaged growth rates and prey abundance implies that prey abundance dominates growth variation at the seasonal scale. It does not imply that temperature and allometric effects do not dominate growth variability on shorter temporal scales or within narrow ranges of prey availability.

Because the goal of this research is to understand the processes that produce variability in growth, we will now focus on the physiological and ecological processes involved in growth. In general, growth is the result of two processes: energy acquired through consumption minus energy expended in metabolism. Energy acquired through consumption is simply the product of the energy density of prey and consumption rate minus the energy lost through egestion and excretion. The energy costs of metabolism include the costs of activity, those associated with the locomotory costs of searching for prey, and those involved in specific dynamic action. The time and energy budgeting processes explicit in the type-2 functional response (Holling 1965; Walters 1986) suggest that there should be a negative relationship between the energetic costs of foraging and both prey consumption and prey abundance. In contrast, Kerr (1982) has suggested a positive relationship between total metabolic rate and ration for two reasons. Kerr (1982) argues that increased ration implies both increases in specific dynamic action and increases in activity metabolism associated with foraging. Kerr (1982) is able to balance an empirical energy budget with the combination of these two mechanisms

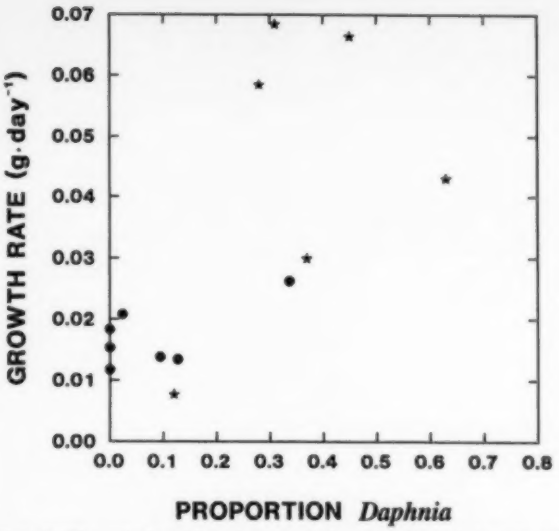

FIG. 9. The relationship of mean daily growth rates in natural lake (stars) versus enclosures (dots) cohorts of YOY yellow perch as a function of the proportion of the total zooplankton biomass that is *Daphnia*.

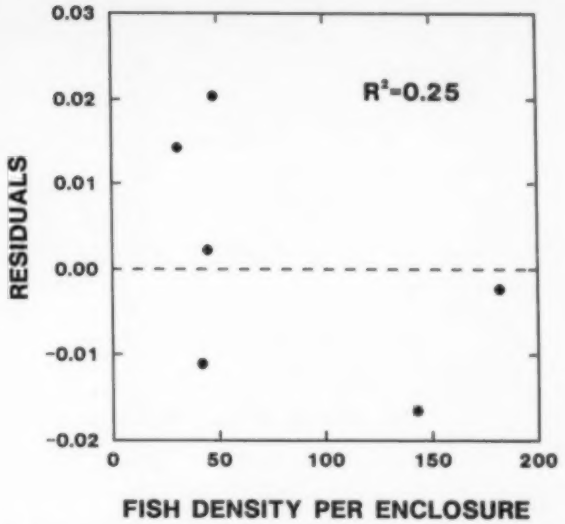

FIG. 10. The residuals from the enclosure growth versus zooplankton biomass relationship plotted as a function of YOY yellow perch density in the enclosures.

although it is not clear which is responsible for the positive relationship between total metabolism and ration. Kerr (1982) is clearly correct when he states that, over the short time scale of foraging bouts, consumption rate and the energetic costs of foraging are positively related. What is less clear is the net energetic cost of foraging over longer (daily) time scales, during which individuals divide their time and energy expenditure between active foraging and relative inactivity. Our simple mechanistic model suggests that Kerr's (1982) proposed positive relationship would have the effect, over longer time scales, of dampening variability in growth owing either to the quantity of prey consumed or to prey availability. It was this inconsistency that lead Hayward (1990) to pose the question "can eating really stunt your growth?" in response to Boisclair and Leggett (1989a). Because our empirical relationships demonstrated an order of magnitude range in growth amongst cohorts that was strongly and positively related to prey abundance, we propose that a negative relationship between the energetic costs of foraging and both prey consumption and prey abundance is more likely than the relationship posed by Kerr (1982).

Our model provides simple predictions that could be tested to differentiate experimentally between these two foraging cost hypotheses. Our hypothesis, of a negative relationship between foraging cost and prey consumption and prey availability, implies that conversion efficiency varies in a positive curvilinear way with prey consumption and prey availability. Kerr's (1982) competing hypothesis implies an invariant conversion efficiency. However, empirical estimates of conversion efficiency must be precise to differentiate between these two competing hypotheses because energy budgets are constrained to generate estimates that are within the relatively narrow envelope of those that are physiologically and ecologically possible (Kerr 1982).

Other processes involved in foraging may cause variability in growth rates. Optimal foraging theory suggests that there is an optimum size of prey that provides the maximum net energy per unit biomass and that smaller and larger prey items provide less net energy per unit weight (Kerr 1971b; Werner and Hall 1974; Stephens and Krebs 1986). YOY yellow perch select intermediate sizes *Daphnia* even though they are capable of capturing larger prey (Mills et al. 1984). In the field, *Daphnia* were preferentially selected and high growth rates were sustained only if *Daphnia* was abundant. In years when *Daphnia* were less abundant, YOY yellow perch switched to larger benthic invertebrates but growth was slower (Mills and Forney 1981). Our lake and enclosure data also suggested that *Daphnia* are important in sustaining high growth rates. At equivalent zooplankton biomasses, YOY yellow perch grew faster in the pelagic enclosures than in the natural lakes when zooplankton abundance was high. The growth differential was related to the higher proportion of *Daphnia* within the zooplankton community in the pelagic enclosures than in the lake littoral zones where YOY yellow perch generally spend most of their first growing season.

Optimal foraging theory would also suggest that, as a predator grows, it should shift to larger prey items to sustain maximum growth rates (Wilbur 1988). Ontogenetic changes in diet of YOY fish are often associated with habitat shifts (Werner 1988). In YOY yellow perch, larvae are pelagic and juveniles switch to the littoral or demersal zone once they attain 25–30 mm in total length (see Post and McQueen 1988 for a review; Wu and Culver 1992). The habitat shift to the littoral or demersal zones is often accompanied by the inclusion of benthic invertebrates in the diet although it has not been established whether the diet shift is in response to characteristics of the prey community or in response to predators (Post and McQueen 1988). In Lake Erie, YOY yellow perch switch from primarily planktivory to benthivory coincident with midsummer declines in zooplankton biomass, and growth rates decline after the switch (Wu and Culver 1992). What is clear from our enclosure experiments is that zooplankton alone are sufficient to produce growth

rates higher than observed in many North American lakes. Therefore, the frequently observed diet shift in YOY yellow perch from zooplankton to larger benthic invertebrates is not necessary to sustain high growth rates.

Examination of growth versus prey biomass for two of the natural cohorts in lakes is particularly interesting. The YOY yellow perch in Eaton Lake switched to benthic invertebrates to a larger extent than the fish in any of the other lakes. Eaton Lake is dominated by a dense population of bluegill sunfish, *Lepomis macrochirus*, that substantially deplete the zooplankton community in both the pelagic and littoral zones. Therefore, intense interspecific competition may explain the diet shift. This result is similar to the diet shift observed in YOY European perch, *Perca fluviatilis*, when competing with roach, *Rutilus rutilus* (Persson 1987; Persson and Greenberg 1990a, 1990b). It is not known if there is an active segregation between *Perca* and their competitors or if *Perca* simply responds to the low availability of zooplankton and switches its diet to benthos. Unfortunately, data on benthic invertebrates were not available for Eaton Lake. The 1984 cohort of YOY yellow perch from Lake St. George also showed an interesting growth pattern. The 1984 cohort was greater than twice as dense (in September) as was the 1985 cohort (McQueen et al. 1989). In July through September 1984, paired offshore purse seining and littoral beach seining showed that the 1984 cohort was made up of two subpopulations with different growth rates and nonoverlapping length distributions (J.R. Post, unpublished data). The offshore subpopulation grew more slowly and fed exclusively on zooplankton. The nearshore subpopulation grew more quickly and showed a partial diet shift to benthic invertebrates. The mechanisms involved in the segregation of the subpopulations are unknown but the suggestion is that the response is density dependent as the lower density 1985 cohort showed the more typical ontogenetic pattern of a short pelagic residence followed by a complete habitat shift to the littoral zone as juveniles (Post and McQueen 1988). Both the pelagic and littoral subpopulations of the 1984 cohort were smaller in body size than the 1985 cohort, also suggesting density-dependent growth mediated through intra-age-class competition and top-down control on invertebrate biomass.

Our discussion so far has focused on the mechanisms that link growth rate to prey availability. Prey availability can be strongly modified by density-dependent processes through exploitative competition (Walters and Post 1993). In addition, the energetic costs of interference competition could modify the relationships among growth, conversion efficiency, and prey abundance (Boisclair and Leggett 1989c). Interference costs can certainly be high in stream salmonids defending territories (Li and Brocksen 1977; Feldmeth 1983; Fausch 1984; Fausch and White 1986) and in reproductively active fish defending nests (Feldmeth 1983; Hinch and Collins 1991) but it is not clear that interference is generally an energetically costly behaviour. It is possible that variation among populations in the level of interference competition could explain some of the variation in growth rates (Boisclair and Leggett 1989c, 1989d). In our enclosure experiments, fish density, and therefore the potential for the intensity of interactions, explained 25% of the variability of residuals from the growth versus prey variability relationship suggesting that the energetic costs of interference may explain about 2% of the observed variability in growth between enclosures. A similar analysis for the natural lake cohorts could not be done because reliable density estimates were not available. This low estimate of the costs of interference competition should not be surprising considering that yellow perch are a shoaling species (Hergrender and Hasler 1968; Nursall 1973; Emery 1973) and may actually benefit from social facilitation and/or predator avoidance (Pitcher 1986; Morgan and Colgan 1987). On the other hand, species for whom interference competition is more pronounced may experience interference costs sufficient to reduce growth rates, and if the magnitude of the interference varied between populations, variation in growth rates could result.

We conclude that most of the growth variability among cohorts within populations and among populations is due to variability in the availability of prey as mediated through density-dependent exploitative competition. The energetic costs of foraging will increase the variation in growth rates if the time and energy budgeting explicit in the type-2 functional response is appropriate. Density-dependent variability in interference competition explained only a small proportion of growth variability in YOY yellow perch. The energetic costs of interference competition are expected to have the greatest negative effect on growth and conversion efficiency at low prey abundance and minimal effect at high prey abundance. Temperature variation in our data set was small and did not explain any of the observed growth variability, but we expect that wider ranges in temperature would effect growth rates. We, therefore, propose that additional field studies aimed at understanding intercohort or interpopulation variation in growth focus initially on prey availability as the most parsimonious hypothesis. Powerful tests of this hypothesis necessitate a data set including a wide range of observations (an order of magnitude in this study) for both the independent and dependent variables.

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A Niche Definition for Lake Trout (*Salvelinus namaycush*) and Its Use to Identify Populations at Risk[1]

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Lake trout (*Salvelinus namaycush*) populations require cold water with high dissolved oxygen content for survival. We developed models that predict the availability of such habitat, using lake mean depth, which describes both the thermal regime and the initial oxygen reserves, and using a measure of primary productivity, which defines the subsequent oxygen demand of the sediments and water column. Measures of primary production include either phosphorus concentration, chlorophyll *a* concentration, or Secchi disk transparency. The models are presented as a series of seasonal oxygen depletion isopleths that predict the extent to which the oxygen content of thermally suitable habitat is lost during the period of thermal stratification. The presence or absence of native lake trout in lakes of northwestern Ontario superimposed on these graphs indicated that natural populations seldom occur in lakes in which the seasonal oxygen depletion exceeds 40%. This isopleth is a niche boundary in its representation of adverse temperature and oxygen conditions for lake trout. The delineation of this boundary permits the identification of lakes where lake trout populations could be seriously affected by cultural eutrophication, overfishing, or climate warming.

Pour survivre, les populations de truite grise (*Salvelinus namaycush*) ont besoin d'une eau froide à teneur élevée en oxygène dissous. Nous avons développé des modèles qui prévoient la disponibilité d'un tel habitat en utilisant la profondeur moyenne du lac, qui décrit à la fois les conditions thermiques et les réserves initiales d'oxygène, et aussi en mesurant la productivité primaire, qui définit la demande subséquente en oxygène des sédiments et de la colonne d'eau. Les mesures de productivité primaire comprennent soit la concentration de phosphore, la concentration de chlorophylle *a* ou la transparence mesurée au disque de Secchi. Les modèles sont présentés sous forme d'isoplèthes de déperdition saisonnière d'oxygène qui prévoient dans quelle mesure la teneur en oxygène de l'habitat aux conditions thermiques appropriées diminue au cours de la période de stratification thermique. La présence ou l'absence de truite grise indigène dans les lacs du nord-ouest de l'Ontario qui est superposée sur les graphiques indique que les populations naturelles existent rarement dans les lacs où la déperdition saisonnière d'oxygène dépasse 40%. Cette isoplèthe délimite la niche écologique par sa représentation des conditions défavorables de température et d'oxygène pour la truite grise. Cette délimitation permet d'identifier les lacs où les populations de truite grise pourraient être gravement touchées par l'eutrophisation, la surpêche ou le réchauffement climatique.

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The natural distribution of lake trout (*Salvelinus namaycush*) in North America is primarily dependent on this species' requirements for cold water and relatively high concentrations of dissolved oxygen (Martin and Olver 1980). Estimates of their temperature preferendum range between 10 and 12°C (Ferguson 1958; McCauley and Tait 1970; Peterson et al. 1979), and it has been suggested that the dissolved oxygen level should be at least 5.5 mg/L to protect lake trout at all life stages (Magnuson et al. 1979). MacLean et al. (1990) used an upper temperature limit of 15.5°C and a lower oxygen limit of 4 mg/L to define "usable" lake trout habitat, while values to 10°C and 6 mg/L were used to define "optimum" lake trout habitat. During summer, such conditions occur only in the hypolimnion and metalimnion of Ontario lakes.

The amount of lake trout habitat present in lakes is important to fisheries managers. Lake trout have become extinct in a number of lakes in central and eastern Ontario where the volume of optimum summer habitat was limited or absent (MacLean et al. 1990). Marshall and Ryan (1987) reported that in northwestern Ontario lakes, the contribution of lake trout to an index of community composition varied with lake mean depth, as it represented the change in vertical extent or volume of lake trout habitat. The productivity of lake trout stocks in central and eastern Canada (as commercial yield) depend on the volume of suitable habitat (Christie and Regier 1988) or on sport fishing effort and the volume of suitable habitat during summer (MacLean et al. 1990).

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The volume of lake trout habitat present in a lake during the period of stratification depends upon the initial oxygen supply at spring overturn, the rate of oxygen depletion through the period of stagnation, and the time between mixing events (Charlton 1980; Cornett and Rigler 1980). These processes can be described or predicted by a number of empirical models. The absolute quantity of oxygen stored at the time of stratification may be represented by the thickness of the hypolimnion, which, in turn, is closely related to lake depth for lakes of similar volume development (Walker 1979). The rate of areal hypolimnetic oxygen depletion (AHOD, expressed as grams of oxygen consumed per square metre of lake surface per day) is associated with the quantity of particulate organic matter present, which is governed by the lake's primary productivity. Numerous studies have demonstrated a relationship between AHOD and trophic indices which are correlates of primary productivity, such as phosphorus concentration, chlorophyll *a* concentration, and Secchi disk transparency (Lasenby 1975; Walker 1979; Charlton 1980; Cornett and Rigler 1980). Finally, the temperature of the hypolimnion, which also affects AHOD, is negatively correlated with lake depth (Cornett and Rigler 1979; Cornett 1989).

Lake depth is clearly a primary factor regulating lake trout habitat, through its control of the thermal regime and the initial oxygen supply. Primary productivity (or one of its correlates) represents a secondary factor regulating habitat suitability, by controlling the rate of oxygen depletion, and hence dictating the late-season oxygen supply. It follows that better predictive models of lake trout habitat might be developed by combining these two metrics. Such models would allow the classification of lakes as to their relative ability to sustain populations of lake trout, and would illustrate how this status might change with a shift in the regulating factors.

In this paper, we develop such models and describe their use. Input parameters include lake mean depth combined with one of three trophic indices: either total spring phosphorus concentration, summer chlorophyll *a* concentration, or summer Secchi disk transparency. The models graphically illustrate the manner in which these variables dictate the seasonal oxygen depletion in lakes, hence the availability of late summer habitat for lake trout. We calibrate the models by comparing the pattern of presence and absence of native lake trout populations in northwestern Ontario lakes, using a simple graphic approach of niche analysis (Hutchinson 1978). Through this process, points are identified along the axes that identify the limits of occurrence for lake trout, hence represent a niche boundary. A second data set is used to verify boundary locations. These graphic models are used to identify lakes in which lake trout populations may be at risk due to cultural eutrophication, climate warming, overexploitation, or other exogenous stresses.

Methods

The extent of oxygen depletion in a lake was described using isopleths determined by lake depth and a trophic index (represented by either spring total phosphorus concentration, summer chlorophyll *a* concentration, or summer Secchi disk transparency), using Walker's (1979) empirical models. There were three steps involved in computing the oxygen depletion isopleths. Initially, AHOD was computed for a range of values for each trophic index, using expressions created by combining Walker's (1979) Equation (6) with his Equation (1), Equation (2), and Equation (3), as follows:

(1) $\log_{10}(\text{AHOD}) = -0.74 + 0.53 \log_{10}(\text{chlorophyll})$

(2) $\log_{10}(\text{AHOD}) = -1.31 + 0.74 \log_{10}(\text{phosphorus})$

(3) $\log_{10}(\text{AHOD}) = 0.14 + 0.72 \log_{10}(1/\text{Secchi} - \alpha)$.

In this last expression, α represents the nonalgal influence on transparency, defined by Walker (1979) as

(4) $\alpha = 0.04 + 0.0025(C)$

where C is the true colour in Pt-Co units. A fixed colour value of 15 Pt-Co units was assumed, which we found to be the mean for lake trout lakes of northwestern Ontario.

The effect of a given AHOD on the depletion of total oxygen reserves is dependent on the thickness of the hypolimnion. In the second step, the thickness of the hypolimnion required to interact with a computed AHOD over a known period of stratification to yield a given level of oxygen depletion (e.g., 10%) was determined, using the expression

(5) $$Z_H = \frac{\text{AHOD} \cdot T_{\text{STRAT}}}{02_{\text{SP}} \cdot (\text{DEP}/100)}$$

where Z_H is the thickness of the hypolimnion (metres), T_{STRAT} is the duration of the period of stratification (days), 02_{SP} is the oxygen concentration at spring overturn (milligrams per litre), and DEP is the percentage seasonal oxygen depletion (percent). Based on our data and that of Schindler (1971), it was assumed that for northwestern Ontario lakes: (1) the depth of the thermocline varies little after its establishment in mid to late May, hence Z_H can be considered a fairly stable quantity; (2) T_{STRAT} could be approximated as 140 d for all lakes; and (3) following spring turnover and the development of thermal stratification, 02_{SP} was 10 mg/L.

As a final step, the lake mean depth that would be required to permit the particular Z_H was predicted by a regression relationship developed from our data as

(6) $Z_H = 2.25Z - 2.62 \qquad r^2 = 0.556,\ n = 75,\ p < 0.01$

where Z is mean depth (metres).

The results of these computations were presented as graphs in which isopleths of percentage seasonal oxygen depletion were a response to the interaction of mean depth and one of the three trophic indices. A shift in the position of the depletion isopleth would be expected as the period of stratification varied across different climatic regions. This effect was illustrated by varying the value for T_{STRAT} in Equation (5). This value was also altered to demonstrate the consequences of climate warming, in addition to an adjustment made to Z_H to compensate for a depression in the thermocline depth.

To determine lake trout niche boundaries, data were collected from two sets of northwestern Ontario lakes (Fig. 1). The West Patricia lake set consisted of 88 lakes situated north of 51°N in the extreme western portion of the province. These lakes were surveyed as part of the Ontario Ministry of Natural Resources (OMNR) lake inventory program. They were quite remote and pristine, and little influenced by anthropogenic phosphorus loading or other cultural stress. Data available for these lakes included mean depth, total spring phosphorus concentration (chlorophyll and Secchi data were unavailable), and the presence or absence of lake trout. Lake trout would have had equal opportunity to

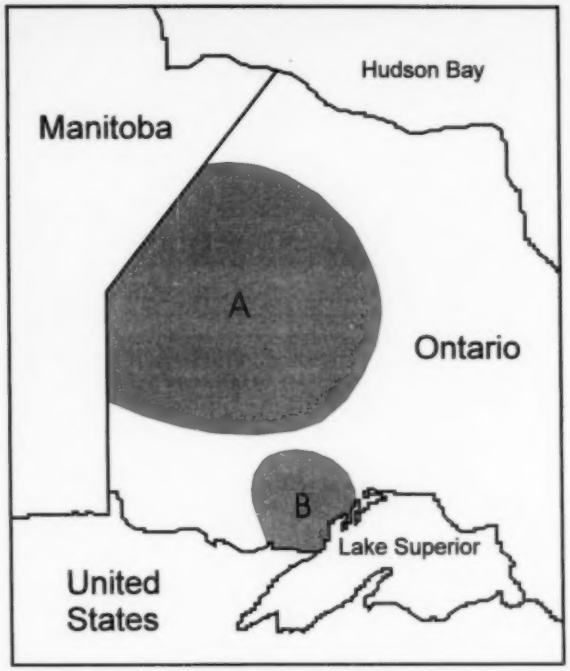

FIG. 1. Location of northwestern Ontario lake sets used in the niche analysis. Area A encompasses the 88 West Patricia lakes used to define the niche boundary, while area B encompasses the 75 research lakes used for model validation.

colonize these lakes (McPhail and Lindsey 1970), and the presence or absence of a lake trout population at the time of survey could be considered to indicate the long term suitability or unsuitability of the lake environment.

Each lake was plotted on the mean depth – phosphorus graph, with the presence or absence of native lake trout populations noted. The niche boundary was determined by visually examining the graph and noting the oxygen depletion isopleth which best separated lakes with and without lake trout populations.

A second data set was used for verification purposes. It consisted of 75 "research" lakes in the vicinity of Thunder Bay, Ont. Similar limnological data were available as for the West Patricia lakes, and in addition, midsummer observations of chlorophyll *a* and Secchi disk transparency. Lake trout would also have had equal opportunity to colonize these lakes, although some populations may have been recently impacted by angling, deforestation, or development within the lake's watershed. The research lakes were plotted on graphs of mean depth – phosphorus, mean depth – chlorophyll, and mean depth – Secchi. The pattern of lake trout presence and absence observed on these graphs was used to validate the oxygen depletion value earlier determined to represent a niche boundary.

Results

The oxygen depletion isopleths illustrated the manner in which lake depth and primary production interacted to determine the extent of late-summer oxygen depletion in the hypolimnion of lakes (Fig. 2). The isopleths were relatively linear for phosphorus, less so for chlorophyll *a*, and curvilinear for Secchi depth. The graphs revealed that a shallow lake must have very low phosphorus or chlorophyll concentration, or high Secchi depth, to ensure that the hypolimnion remained well oxygenated throughout the summer. A deeper lake with the same trophic index (phosphorus, chlorophyll *a*, or Secchi depth) would have provided a

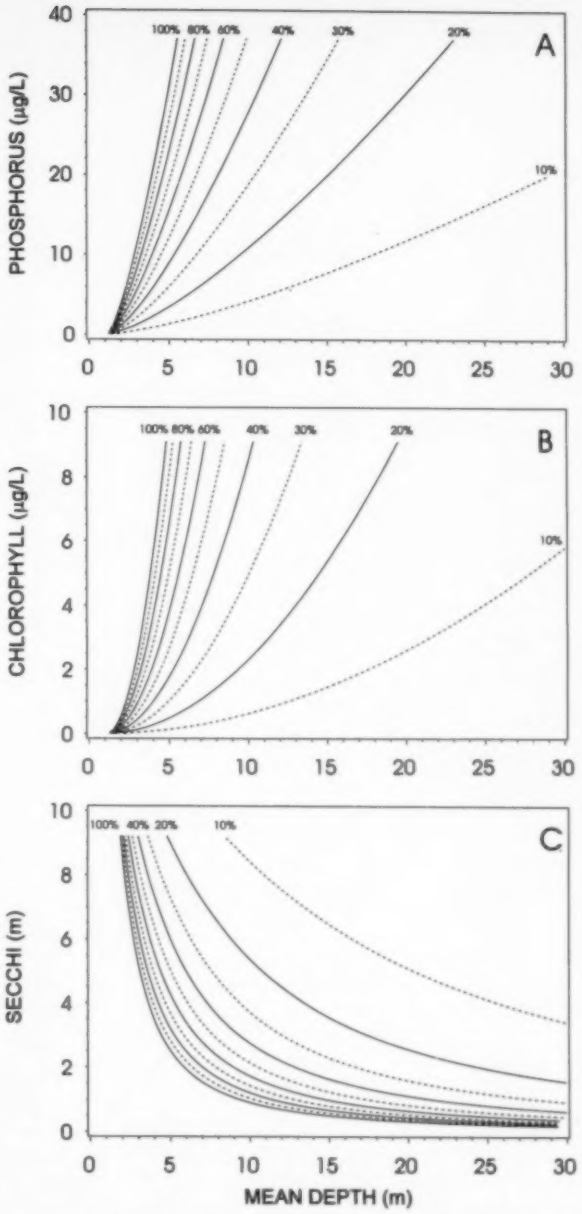

FIG. 2. Isopleths representing the percent depletion of hypolimnetic oxygen over the period of summer stratification, as predicted using empirical models of lake mean depth and either (A) phosphorus concentration, (B) chlorophyll *a* concentration, or (C) Secchi disk depth.

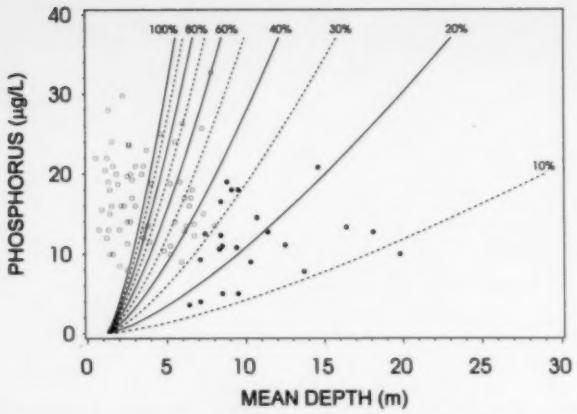

FIG. 3. The presence (solid circles) and absence (open circles) of lake trout in the West Patricia lakes, superimposed over the oxygen depletion isopleths. The legend for the isopleths is the same as Fig. 2.

thicker layer of water suitable for lake trout because of its greater spring storage of oxygen.

Patterns in presence or absence of native lake trout populations in the relatively pristine West Patricia lakes were readily observed when plotted on the mean depth – phosphorus graph (Fig. 3). The isopleth representing an annual oxygen depletion of 30% separated the majority of lakes with lake trout, from those without. Some lakes located between the 30 and 40% isopleths supported lake trout, however; none were found beyond the 40% isopleth, which defined a niche boundary for lake trout, separating lakes that provide suitable temperature and oxygen regimes from those without.

This pattern was confirmed when lake trout presence–absence data from the research lake set were plotted on the graphs of mean depth versus the three trophic indices (Fig. 4). Native lake trout occurred in all lakes (with one exception noted on the chlorophyll – mean depth plot) for which oxygen depletion was predicted to be less than 20%. The zone of overlap between lake trout and non-lake trout lakes was bounded by the 40 and 20% isopleth, which was a wider range than for the West Patricia lakes. Lake trout were present in only one lake for which the seasonal oxygen depletion was predicted to exceed 40%. The second lake set validated the identification of the 40% isopleth as a niche boundary, estimated using any of the three measures of primary production.

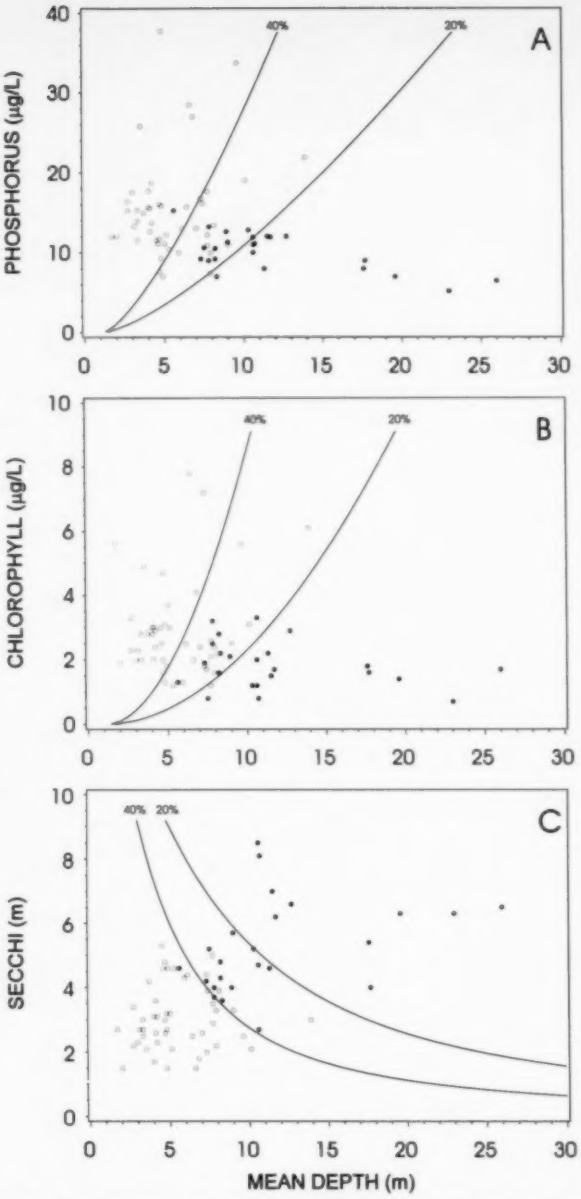

FIG. 4. The presence (solid circles) and absence (open circles) of lake trout in the research lakes, superimposed over the 20 and 40% oxygen depletion isopleths, when plotted against mean depth and (A) phosphorus concentration, (B) chlorophyll *a* concentration, and (C) Secchi disk depth.

Discussion

There was a clear pattern of presence or absence of native lake trout populations when northwestern Ontario lakes were mapped onto axes of primary productivity versus mean depth (Fig. 3 and 4). The occurrence of lake trout in these lakes was assumed to indicate their long term suitability for this species. The absence of lake trout from particular lakes was considered to indicate that environmental conditions were at least periodically inhospitable to lake trout, or alternatively they lacked the physical structure or the mix of biota necessary for the maintenance of lake trout at all life stages. The lake trout presence–absence data were, therefore, interpreted to be the results of long-term natural experiments which have tested the capability of these lakes to support self-sustaining populations of lake trout. Lakes which experienced seasonal oxygen depletion of 20% or less, have apparently provided the thermal and oxygen conditions necessary for the long-term survival of lake trout populations.

Ryder and Edwards (1985) expected lake trout populations to vary in their characteristics if lakes were compared along a phosphorus gradient. Populations would exhibit

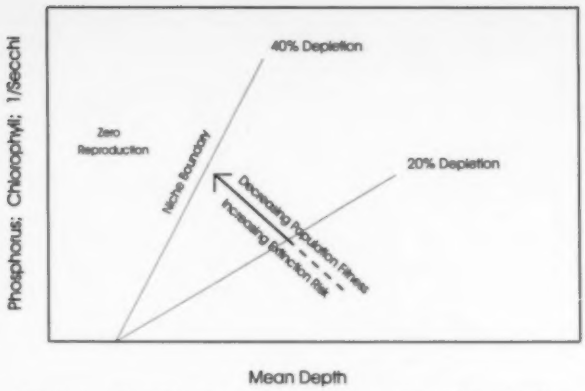

FIG. 5. A schematic view of the niche concept and implications for the fitness and extinction risk of lake trout populations.

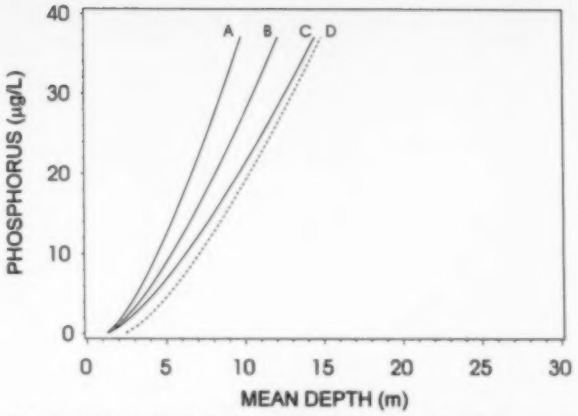

FIG. 6. Shifts in the 40% annual oxygen depletion isopleth caused by reducing or prolonging the period of summer stratification to (A) 110 d, (B) 140 d, and (C) 170 d. Recent climate warming in northwestern Ontario would shift the isopleth from B to D, because the thermocline was moved deeper by 2.5 m and the duration of stratification increased to 161 d.

slow growth and maximum reproduction while experiencing slight competition under ultraoligotrophic conditions. Under oligotrophic conditions, populations would exhibit optimum reproduction and moderate growth while experiencing moderate competition. As conditions approached mesotrophy, both growth and competition would be maximum, while reproduction would be limited because of the effect of organic siltation on spawning habitat. Reproductive success and recruitment to the adult part of the stock can also be influenced by the suitability of habitat during the period of stratification. MacLean et al. (1990) found that reproductive failure had occurred or lake trout were considered extinct in 37 of the 151 lakes located in eastern and central Ontario. Most of these lakes were characterized as having limited habitat or no summer habitat for lake trout. In comparison with this, lakes where natural reproduction of lake trout occurred were found to have significantly more habitat suitable for lake trout. Two factors identified by Evans et al. (1991) have the potential to contribute to reduced population fitness as a consequence of reduced habitat volume. First, gonadal development and gamete production could be impaired if the oxygen concentration was reduced to a level that suppressed feeding during middle to late summer. Second, Evans et al. (1991) found evidence to support a hypothesis that predation by adult trout on young lake trout is a significant mechanism regulating population size and that the extent of the predation is dependent on habitat overlap. Young lake trout were found to inhabit the deepest waters of lakes during the period of stratification. This separated them from the adult fish, which were found higher in the water column. Predation by adult lake trout was found to be a major factor affecting survival of young lake trout in Lake Opeongo. Predation was expected to be increased if the young lake trout were forced out of their deep-water refuge by seasonally adverse conditions of temperature and oxygen, or if habitat overlap occurred owing to limited lake depth. Evans et al. (1991) found that the extent to which lake trout stocks in central Ontario lakes were supported by natural reproduction (percent native fish) varied in accordance with this habitat segregation–overlap hypothesis.

The niche space can be contoured in terms of the biological responses of populations such as maximum rate of reproduction or of population growth (Maguire 1973). The 40% isopleth was identified as a niche boundary for lake trout. The preceding evidence indicates that population fitness is reduced as the niche boundary is approached (Fig. 5). Populations that exist in lakes that map close to the niche boundary are less resistant to stress and predisposed to collapse or extinction due to low fitness.

The oxygen-depletion models were developed to illustrate the joint influence of depth and primary production on the extent of oxygen depletion in the hypolimnion of lakes of northwestern Ontario. The models can, however, be readily adapted for application to other regions. The location of isopleths (Fig. 2) will vary with the mean oxygen concentration at spring overturn, duration of stratification, and thickness of the hypolimnion. An extended stratification period, representative of more southerly climes, would shift the depletion isopleths to the right, as illustrated on the phosphorus – mean depth plot (Fig. 6), whereas the opposite effect would characterize colder climates experiencing a shorter period of stratification. For this reason, lake trout populations in northern regions might be able to persist in lakes that are shallower or more productive than those in southern locales.

The global warming phenomenon has serious implications for native lake trout populations. Schindler et al. (1990) reported that a 2°C increase in mean annual air temperature over the past 20 yr has seriously affected the thermal regimes of lakes in northwestern Ontario. Thermoclines have formed at depths 2–3 m below that previously recorded, resulting in a substantial reduction in the amount of cold-water habitat and oxygen reserves. In addition, the ice-free season has lengthened by approximately 3 wk, which would prolong the period of stratification. These changes would have a major impact on marginal lake trout lakes, and are probably affecting lake trout populations in northern Ontario at present. A longer stratification period coinciding with a reduction in the hypolimnion thickness would result in a substantial shift in the 40% oxygen depletion isopleth (Fig. 6). Lake trout populations in lakes that fall to the left of this repositioned isopleth (i.e., where the seasonal oxygen depletion now exceeds 40%) would be in a position of extreme risk.

Caution should be exercised in the prediction of environmental conditions in small lakes. Lake trout were present in one lake that was predicted to experience a seasonal oxygen depletion in excess of 40% (mean depth 5.6 m, phosphorus concentration 15.2 mg/L and Secchi depth 4.6 m). A large subsurface spring was present in this small (19 ha) headwater lake and probably provided a refugium for lake trout as documented for another Ontario lake (E.J. Snucins and J. Gunn, Laurentian University, Sudbury, ON P3E 2C6, Canada, personal communication). The extent of seasonal mixing is another source of concern in the prediction of conditions in small lakes. The surrounding topography, shape, size, and depth of the basin are primary considerations when determining a lake's susceptibility to mixing (Gorham and Boyce 1989). From surveys of lakes in the Experimental Lakes Area of northwestern Ontario (Schindler 1971) and from our own experience, it is evident that seasonal mixing is more likely to be incomplete in small lakes. Owing to the limited volume of cold water in small lakes, such events can result in a considerable reduction or total absence of habitat suitable for lake trout during late summer.

Management Implications

Specific aspects of the lake trout niche have been defined by mapping out a range of environmental conditions within which natural lake trout populations exist (Fig. 3 and 4). The extent of seasonal depletion of hypolimnetic oxygen can be predicted from knowledge of lake mean depth and a measure of either phosphorus concentration, chlorophyll *a* concentration, or Secchi disk transparency. In instances where mean depth is unknown, the relationship between mean and maximum depths may be used to provide an initial characterization of the lake, and perhaps identify the need for bathymetric survey.

Cultural eutrophication, generated by development or disturbance within an upper watershed, is a serious management concern for lake trout lakes of Ontario (Hutchinson et al. 1991). The oxygen depletion models (Fig. 2) would allow a fisheries manager to determine the current state of a lake. While the 40% oxygen depletion isopleth defines the niche boundary for lake trout, the 20% isopleth may be used as a conservative definition of lake trout habitat. These models can then be used to define a management objective of phosphorus concentration to maintain or improve lake trout habitat. The well-known relationships between phosphorus concentration, loading, and water budgets (e.g., Dillon and Rigler 1974, 1975; Scheider 1978) readily lend themselves to the definition of management prescriptions in regard to permissible loadings.

The depletion models allow us to evaluate the relative risk of extinction of lake trout populations exposed to other exogenous stresses. The 40% oxygen depletion isopleth is a niche boundary for lake trout (Fig. 5). Lake trout populations present in lakes with significant seasonal oxygen depletion should be less resilient to a reduction in their numbers, brought about directly through exploitation or indirectly through competition with introduced or invading species. Similarly, these populations may be unable to compensate for any additional impairment of their reproductive potential caused by the loss of spawning substrate or exposure to contaminants. It would seem that a high degree of regulatory control is required to ensure the perpetuation of native lake trout in marginal lakes.

Evidence from northwestern Ontario (Schindler et al. 1990) indicates that fisheries managers in Ontario and elsewhere should be extremely concerned about the effect of global warming on the status of lake trout populations in marginal lakes. Under the revised climate regime, oxygen reserves in these lakes may no longer be sufficient to sustain lake trout over a longer, warmer summer. Our models can be used to evaluate the impact of local climate-warming scenarios by identifying the lake trout populations in jeopardy, as indicated by the shifted oxygen depletion isopleths (Fig. 6). Some of these populations will certainly be lost, and our only hope of sparing others may be through substantial reductions in nutrient loading.

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Regulation of Rotifers by Predatory Calanoid Copepods (Subgenus *Hesperodiaptomus*) in Lakes of the Canadian Rocky Mountains

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Paul, A.J. and D.W. Schindler. 1994. Regulation of rotifers by predatory calanoid copepods (subgenus *Hesperodiaptomus*) in lakes of the Canadian Rocky Mountains. Can. J. Fish. Aquat. Sci. 51: 2520–2528.

The abundance of planktonic rotifers in alpine lakes is regulated by predation from *Diaptomus* (subgenus *Hesperodiaptomus*) *arcticus* (a large calanoid copepod) regardless of nutrient conditions. We manipulated both predators and nutrient levels in large in situ enclosure experiments (2250 L). *Hesperodiaptomus arcticus* suppressed densities of the soft-bodied rotifer *Polyarthra dolichoptera* significantly (two to three orders of magnitude) and the loricate rotifer *Keratella quadrata* less so (up to one order of magnitude) relative to populations in predator-free enclosures. *Keratella quadrata*'s armoured lorica may limit predation by *Hesperodiaptomus*. Nutrient addition resulted in higher phytoplankton standing crops and rotifer densities but did not permit rotifers to exceed predator consumption. In 69 lakes from the Canadian Rocky Mountains, the presence of *Keratella* or *Polyarthra* was negatively correlated with *Hesperodiaptomus* density. A maximum-likelihood logistic regression model predicts that as *Hesperodiaptomus* densities increase the probability of occurrence for both rotifer genera decreases, with *Polyarthra* declining more rapidly than *Keratella*.

L'abondance des rotifères planctoniques dans les lacs alpins est régulée par la prédation effectuée par *Diaptomus* (sous-genre *Hesperodiaptomus*) *arcticus* (un gros copépode calanoïde), quelles que soient les conditions nutritives. Nous avons manipulé les concentrations de prédateurs et de nutriments dans des expériences à grande échelle réalisées in situ en enclos (2 250 L). *Hesperodiaptomus arcticus* a réprimé la densité du rotifère à paroi souple *Polyarthra dolichoptera* de manière significative (de deux à trois ordres de grandeur) et, dans une moindre mesure, celle du rotifère à coquille *Keratella quadrata* (jusqu'à un ordre de grandeur) par rapport aux populations gardées dans des enclos exempts de prédateurs. La coquille cuirassée de *Keratella quadrata* peut limiter la prédation par *Hesperodiaptomus*. L'ajout de nutriments a provoqué des densités plus élevées des populations sur pied de phytoplancton et de rotifères, mais il n'a pas permis aux rotifères de surpasser la consommation des prédateurs. Dans 69 lacs des montagnes Rocheuses canadiennes, la présence de *Keratella* ou de *Polyarthra* était corrélée de manière négative à la densité de *Hesperodiaptomus*. Un modèle de régression logistique de maximum de vraisemblance prévoit que l'accroissement de la densité de *Hesperodiaptomus* augmente la probabilité de diminution des deux genres de rotifères, *Polyarthra* diminuant plus rapidement que *Keratella*.

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The ability of invertebrate predators to regulate planktonic rotifer communities has been debated. Dodson (1974) hypothesized that invertebrate predators can control zooplankton community structure, keeping small zooplankton scarce by selectively preying on them. Several publications have supported these predictions (Dodson 1974; Hebert and Loaring 1980; Luecke and O'Brien 1983; Vanni 1988); however, all were studies of invertebrate predation on crustacean zooplankton. Although numerous invertebrate predators are known to prey on rotifers (McQueen 1969; Anderson 1970a; Federenko 1975; Hillbricht-Ilkowska et al. 1975; Williamson 1983; Neill 1984; Moore and Gilbert 1987; Yan et al. 1991), their importance in controlling rotifer abundance is either insignificant or unknown. Havens (1990) established that *Chaoborus punctipennis* preyed selectively on rotifers but it had a minimal effect on rotifer community size and structure, most likely because of the high reproductive output of rotifers. In contrast, predation on rotifers by some invertebrates (predacious rotifers, copepods, and *Chaoborus*) has been predicted to be important from empirical studies (Anderson 1977, 1980; Foran and King 1982; Hofmann 1983; Stemberger and Evans 1984), consumption rate estimates (Brandl and Fernando 1979; Williamson 1983; Elser et al. 1987), and enclosure experiments (Arnott and Vanni 1993).

The role of competitors in limiting populations of herbivorous rotifers has been better studied. There is little doubt that large *Daphnia* can control rotifer populations (see Gilbert 1988 for a review). Neill (1984) determined that rotifer biomass was more strongly regulated by the presence of the competitor (*Daphnia*) than by predaceous calanoid copepods; in fact, *Chaoborus trivittatus* predation on *Daphnia* enhanced rotifer biomass through competitive release, even though *C. trivittatus* is also known to prey on rotifers (Neill and Peacock 1980). Predators may only "fine tune" rotifer abundance when rotifers are already constrained by a low food limit set by crustacean grazing (Neill 1984).

The importance of invertebrate predation on rotifer populations is dependent on rotifer production (Yan et al. 1991). Generation time and brood size (one or two amictic eggs) of rotifers have been shown to be directly related to food supply

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FIG. 1. Study area showing location of lakes. ⊗ = Snowflake Lake (site of enclosure experiments) and lakes used for distributional data (★ = lakes sampled in this study; ■ = lakes from other reports).

(Makarewicz and Likens 1979). Consequently, predators might be able to control rotifer abundance if rotifer reproduction is food limited. We hypothesized that low food availability in ultra-oligotrophic alpine lakes might lower the reproductive rates of rotifers enough to allow control by invertebrate predators.

The objectives of our study were threefold. First, we tested the hypothesis that *Diaptomus* (subgenus *Hesperodiaptomus*) *arcticus*, a large (2–3 mm) predatory calanoid copepod, can regulate rotifer populations in alpine lakes of the Canadian Rocky Mountains. Anderson (1977, 1980) previously showed a negative correlation in the distribution of *Hesperodiaptomus* and rotifers in these lakes indicating the potential for predatory regulation. Second, we tested whether elevated nutrient supplies could indirectly decrease the ability of *Hesperodiaptomus arcticus* to control rotifer populations by increasing food availability for rotifers. These two hypotheses were tested in enclosures by manipulating predator densities and nutrient concentrations. The experiments were carried out in Snowflake Lake (51°35′N, 116°50′W) in Banff National Park, Alberta. Finally, our findings from the enclosure experiments were compared with the distribution of *Hesperodiaptomus* and rotifers in 69 lakes of the Canadian Rocky Mountains.

Methods

Study Lakes

The 69 lakes are situated in the Canadian Rocky Mountains east of the continental divide within Willmore Wilderness Area, Jasper National Park, and Banff National Park (Fig. 1). Previous data were available for 63 of these lakes (Anderson 1971, 1974; Donald 1987; D. Donald, Environment Canada, 2365 Albert Street, Regina, Sk S4P 4K1, unpublished data). The lakes ranged in elevation from 1024 to 2423 m, in maximum depth from 1.5–96 m, and in area from 0.2–2066 ha. Forty five of the lakes were known to have been stocked with fish during the 20th century, although most of these lakes initially had no fish. The fate of stocked fish in the lakes varied from successful introductions to complete failures (Donald 1987). The remaining 24 lakes were never stocked and only four of these have natural fish populations.

Snowflake Lake is relatively small (7.13 ha), deep (12.5 m), and alpine (elevation 2320 m), and is located

between the Vermilion and Bare ranges of the Rocky Mountains in Banff National Park (Fig. 1). Prior to 1960, the zooplankton assemblage consisted of *H. arcticus* and *Daphnia pulex* with small numbers of *Diaptomus tyrelli*, *Acanthocyclops vernalis*, and rotifers (*Kellicottia longispina*: Anderson 1972). From 1960 to 1966 the lake was stocked with rainbow trout (*Oncorhynchus mykiss*, brook trout (*Salvelinus fontinalis*), and cutthroat trout (*Oncorhynchus clarki*) (Anderson 1972). Large crustaceans (*H. arcticus* and *D. pulex*) were eliminated by fish predation. Small copepods (*A. vernalis*, *D. tyrelli*, and *Diacyclops bicuspidatus thomasi*) and cladocerans (*Chydorus sphaericus*) increased in density, shifting the size structure of the zooplankton community toward much smaller species (Anderson 1972, 1974). The fish did not reproduce and apparently disappeared from the lake by the late 1970s or early to middle 1980s (D. Donald, Environment Canada, 2365 Albert Street, Regina, SK S4P 4K1, personal communication). *Daphnia pulex* became re-established in the lake by 1974 and was collected in subsequent years; however, *H. arcticus* has not returned to Snowflake Lake and the pelagic community remains dominated by small-bodied species, with *D. pulex* being the only large species present (A.J. Paul and D.W. Schindler, unpublished data).

Distribution of *Daphnia* and Rotifers in Snowflake Lake

Densities of *D. pulex* and the dominant rotifers were determined during the ice-free season (late June – early October) for Snowflake Lake in 1991 and 1992. Weekly collections were made using a plankton net (25-cm diameter, 64-μm mesh) towed vertically five times from 11 m to the surface. Samples were preserved in formalin–sucrose (Prepas 1978). Zooplankton were enumerated from separate subsamples using a dissecting microscope for *D. pulex* and an inverted microscope for rotifers. No fewer than four subsamples for both *Daphnia* and rotifers were counted. The volume of each subsample ensured that at least 50 individuals of the dominant species were present. A random distribution of subsample counts was determined with a χ^2-test of the variance to mean ratio (Prepas 1984). The coefficient of variation was <20% for each species counted, except when a species was rare. Plankton net efficiency was set at 20% from values calculated by Anderson (1970b) using a similar net in lakes of Jasper National Park. We stress that the densities obtained for rotifers are subject to inaccuracies associated with plankton nets and rotifer sampling (Green 1977). Our density estimates likely only represent changes in order of magnitude and even at this level soft-bodied species, such as *Polyarthra*, may be underestimated (Green 1977).

Enclosure Experiments

During 1991 we used six enclosures to test the effect of *H. arcticus* predation on the plankton community of Snowflake Lake. The enclosures were square (0.9 × 0.9 × 3 m) and constructed of woven polyethylene closed at the bottom with a volume of 2250 L when filled. They were suspended from floating frames constructed of ABS plastic pipe. *Hesperodiaptomus arcticus* were added to triplicate predator addition enclosures to achieve a density of 1.6 individuals·L^{-1}; three reference enclosures received no *H. arcticus*. The stocked density of *H. arcticus* is less than the mean (3.2 individuals·L^{-1}) for 20 lakes with *Hesperodiaptomus* in the Canadian Rocky Mountains (D. Donald, Environment Canada, 2365 Albert Street, Regina, SK S4P 4K1, unpublished data). One predator addition enclosure was lost in a storm.

Hesperodiaptomus arcticus were collected from Pipit Lake (2 km north of Snowflake Lake) and transferred to appropriate enclosures in Snowflake Lake 5 d after ice-out, on the 15th of July (day 0 of the experiment). *Hesperodiaptomus arcticus* were collected from Pipit Lake using a coarse-mesh (1-mm) large-diameter (36-cm) zooplankton net. The mesh separated large bodied *H. arcticus*, *Gammarus lacustris* (>5 mm), and *Daphnia middendorffiana* (≈3 mm) from smaller taxa. The latter two species occurred at low densities (<0.01 individuals·L^{-1}) and were easily removed by further filtration through a 3-mm mesh and hand picking. The duration of the experiment was 36 d. Enclosures were sampled at approximately 4-d intervals.

In 1992 we tested the interactive effects of *H. arcticus* predation and nutrient addition on the planktonic community of Snowflake Lake. The experimental design was a two by two factorial analysis with three replicates (total of 12 enclosures). The treatments were predators (*H. arcticus*), nutrients (N and P), both predators and nutrients, or neither. *Hesperodiaptomus arcticus* were collected from Pipit Lake in a manner similar to the 1991 experiment, except that a larger collecting net was used (120 cm diameter). This allowed us to stock *H. arcticus* in the enclosures at densities similar to the mean for 20 mountain lakes with *Hesperodiaptomus* (3.2 individuals·L^{-1}). Nutrients were added as NH_4NO_3 and H_3PO_4 (30:1 N:P by atomic ratios) to increase total phosphorus (TP) by a factor of four; natural TP and total nitrogen in Snowflake Lake are ≈4 and ≈120 μg·L^{-1}, respectively. Concentrations were maintained at constant values by weekly additions of NH_4NO_3 and H_3PO_4 as required. Both nutrients and *H. arcticus* were added to the enclosures on 27 June (day 0) approximately 1 wk after ice-out. The experiment ran for 36 d and the enclosures were sampled at weekly intervals.

Water samples were collected in 1991 and 1992 from the enclosures and the lake (near the enclosures) using a clear polyvinylchloride tube 2.75 m in length and 0.05 m inner diameter (deVries and Stein 1991). The tube was dropped vertically into each enclosure or the lake, plugged at the top, removed quickly, and emptied into a bucket. The procedure was repeated once removing approximately 10.5 L of water, or about 0.5% of the enclosure volume. From the 10.5 L, aliquots were taken for algal pigment analysis (0.5–1 L) and TP (0.25 L). The remaining volume was used for enumeration of rotifers and crustaceans. Zooplankton were concentrated through a 10-μm mesh, washed into vials, and preserved in a formalin–sucrose (Prepas 1978). The minimum detectable limit for plankton using the tube sampler (assuming a Poisson distribution and a 95% probability of detection) is 0.1 individuals·L^{-1}. Larger samples were not taken to minimize depletion effects on enclosure populations.

Zooplankton species were identified using keys from Edmondson (1959), Chengalath et al. (1971), Ruttner-Kolisko (1974), Grothe and Grothe (1977), and Pennak (1978). Zooplankton were enumerated by allowing the entire sample to settle for 24 h, and then counting all individuals using an inverted microscope. Algal biomass was inferred from concentrations of chlorophyll *a* (chl *a*) and quantified by high performance liquid chromatography (HPLC; Leavitt and Carpenter 1990). Rotifer densities were compared among treatments using one-way or two-way repeated measures

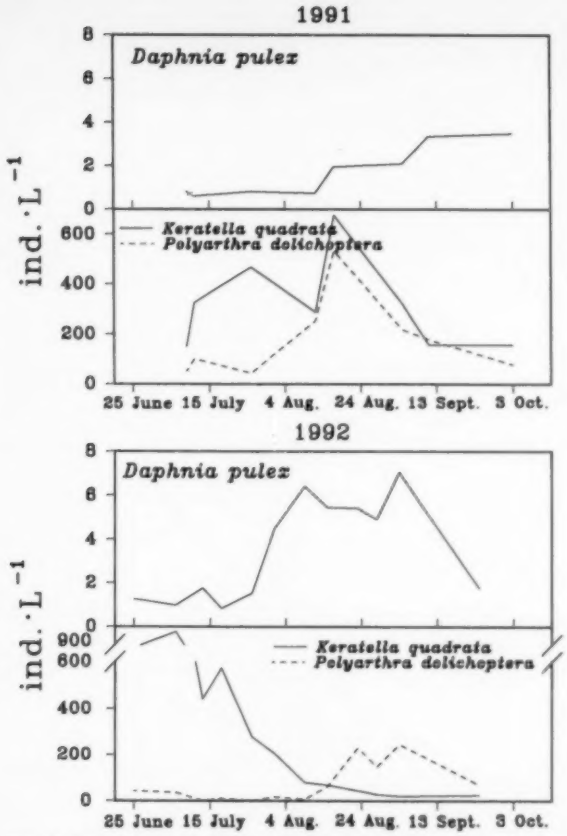

FIG. 2. Densities of dominant rotifers and *Daphnia pulex* in Snowflake Lake for the ice-free seasons of 1991 and 1992. Densities were estimated from samples collected with a plankton net at the deepest point in Snowflake Lake.

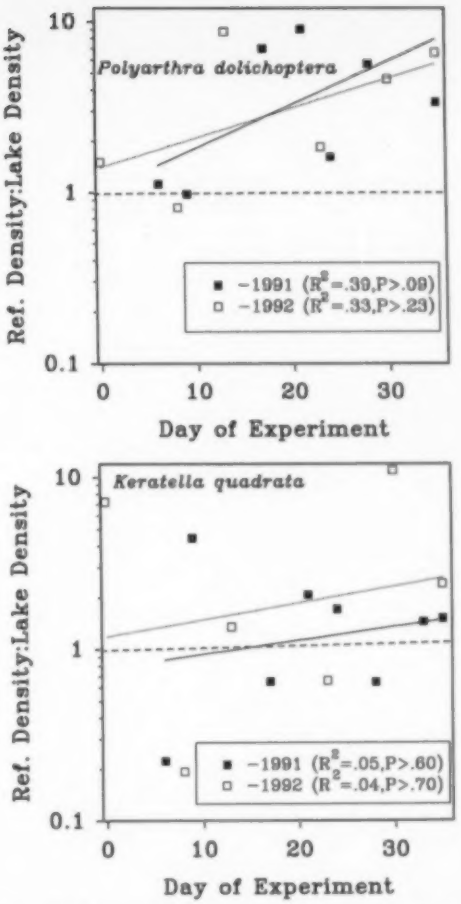

FIG. 3. Ratio between mean densities of the rotifers *Polyarthra dolichoptera* and *Keratella quadrata* for reference enclosures (no predators or fertilizer) and Snowflake Lake for 1991 and 1992. Densities are equal when the ratio is 1 (dashed line). Coefficients of determination and probabilities regression slopes are not different from zero and are shown for both years (solid line = 1991; broken line = 1992).

analysis of variance with fixed effects (Sokal and Rohlf 1981). Rotifer densities were $\log_{10}$ transformed before statistical analysis because means increased exponentially and were positively correlated with variance (Sokal and Rohlf 1981). Exponential growth was determined by linear regression of transformed data. Statistical significance for tests was set at $\alpha = 0.05$; probabilities are given for all tests.

Geographic Distribution Data

We related the occurrence of rotifers to the densities of *Hesperodiaptomus* in 69 lakes of the Canadian Rocky Mountains (Fig. 1). Plankton samples in all cases were collected with a plankton net (0.25-m diameter, 64-μm mesh) towed from 1 m above the bottom to the surface over the deepest area of each lake. Densities of *Hesperodiaptomus*, averaged over ice-free months (June–September), were corrected for net efficiency using coefficients from Anderson (1970b). Only the presence or absence of rotifers was determined because of the inaccuracy involved in quantitative assessments of rotifers, especially when using plankton nets (Green 1977).

Maximum-likelihood logistic regressions (Pindyck and Rubinfeld 1981) were used to model the presence or absence of rotifers as a function of *Hesperodiaptomus* density. This analysis was chosen over least-squares regression analysis because the dependent variable (presence–absence of rotifers) is dichotomous (Reckhow et al. 1987). Parameters from the regression analysis were fit to the logistic model:

$$(1) \quad P(y) = \frac{1}{1 + e^{-(a+b(x))}}$$

where $P(y)$ is the probability of the rotifer species being present, x is the density of *Hesperodiaptomus* ($\log_{10}$ density + 0.01), a is the intercept, and b the slope. The statistical validity of the model was tested using χ^2 goodness-of-fit (SAS Institute Inc. 1988), with $\alpha = 0.05$.

Results

Distribution of *Daphnia* and Rotifers in Snowflake Lake

The zooplankton in Snowflake Lake during 1991 and 1992 consisted largely of *Diacyclops bicuspidatus thomasi*, *Diaptomus tyrelli*, *Daphnia pulex*, and rotifers. These three

Table 1. Repeated measures analysis of variance for log-transformed densities of *Polyarthra dolichoptera* and *Keratella quadrata* from enclosures in 1991. Treatment refers to presence or absence of the predator *Hesperodiaptomus arcticus*.

Test	Source	df	MS	*P*
Polyarthra dolichoptera	Treatment	1	62.143	0.002
	Error	3	0.535	
Keratella quadrata	Treatment	1	7.344	0.226
	Error	3	3.176	

crustacean species were reported by Anderson (1972, 1974) to be present in Snowflake Lake at some point following fish stocking. The dominant planktonic rotifers were *Polyarthra dolichoptera* (120 × 76 μm) and *Keratella quadrata* (126 × 72 μm). We also collected *Keratella cochlearis*, *Synchaeta* spp., *Notholca* spp., *Testudinella* spp., and *Kellicottia longispina*. The genera *Keratella*, *Notholca*, and *Testudinella* were not previously reported from Snowflake Lake (Anderson 1972).

Densities of *D. pulex* did not exceed 1 individual·L^{-1} until late July to mid-August of each year (Fig. 2). The maximum density of *D. pulex* was 3 or 4 individuals·L^{-1} in 1991 and 6 or 7 individuals·L^{-1} in 1992. Densities of the dominant rotifers (*K. quadrata* and *P. dolichoptera*) tended to decrease as *D. pulex* increased (Fig. 2); however, the peak densities of *P. dolichoptera* and *D. pulex* in 1992 occurred simultaneously (Fig. 2).

Enclosure Experiments

Rotifer densities in the reference enclosures (no predators or nutrients) and the open lake followed similar trends. The two dominant pelagic rotifer species (*P. dolichoptera* and *K. quadrata*) were always present at densities greater than 0.1 individuals·L^{-1}. The ratios of mean density in reference enclosures to lake samples for the dominant rotifers were not significantly related to time in either 1991 or 1992 (Fig. 3). If rotifers in the enclosures and the lake did not follow similar growth patterns (i.e., one increased at a greater rate), then the ratios of mean reference enclosure density to lake density would have increased or decreased over time. During both years, *P. dolichoptera* and *K. quadrata* reached higher densities in the enclosures than in lake samples; however, the difference was always less than an order of magnitude, except for *K. quadrata* on one date in 1992 (Fig. 3).

Naupliar stages of *H. arcticus* were collected infrequently and copepodids were never detected in any of the enclosures in both 1991 and 1992. Therefore, any change in net *H. arcticus* predation rates represented a functional response of the predator and not a numerical response.

Predator Effects

In the 1991 experiment, enclosures with *H. arcticus* (predator addition) had significantly lower densities of *P. dolichoptera* than reference enclosures (Table 1; Fig. 4). *P. dolichoptera* rarely exceeded densities >0.1 individuals·L^{-1} in predator-addition enclosures but increased exponentially with time in the reference enclosures (Fig. 4; R^2 = 0.97, df = 7, $P < 0.0001$). *Keratella quadrata* densities did not differ significantly in either the reference or predator-addition enclosures (Table 1; Fig. 4).

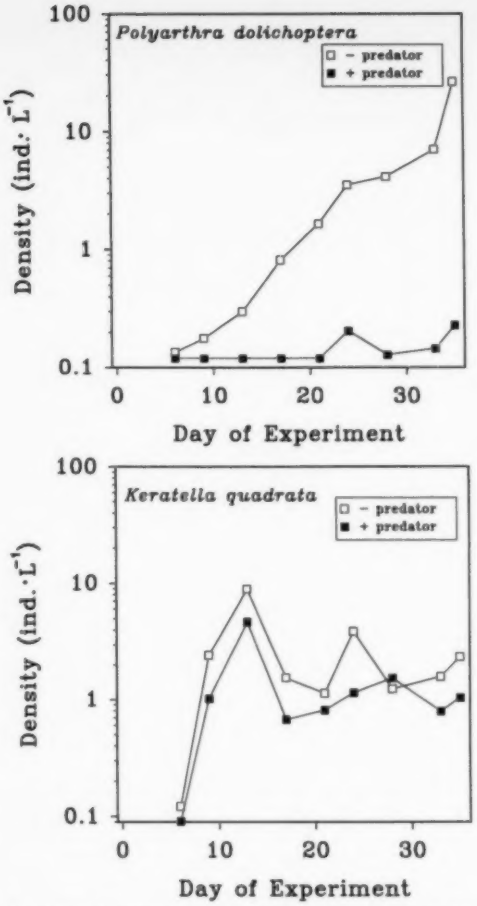

FIG. 4. Mean densities of the dominant rotifers *Polyarthra dolichoptera* and *Keratella quadrata* in enclosures with or without the predator *Hesperodiaptomus arcticus* for 1991. Samples taken on day 0 were lost so there are no data points for day 0.

Predator additions in 1992 again significantly lowered *P. dolichoptera* densities (Table 2; Fig. 5). *P. dolichoptera* densities remained low when the predators were present, regardless of nutrient addition (Fig. 5). In contrast, exponential growth of *P. dolichoptera* occurred in both fertilized (R^2 = 0.90, df = 4, $P < 0.004$) and unfertilized (R^2 = 0.97, df = 4, $P < 0.0005$) enclosures without predators (Fig. 5).

In 1992 predator addition significantly reduced the densities of *K. quadrata* in all enclosures (Table 2; Fig. 5). Predators reduced densities up to an order of magnitude in both fertilized and unfertilized enclosures (Fig. 5). *Keratella quadrata*, however, increased exponentially in fertilized treatments with predators (R^2 = 0.78, df = 4, $P < 0.02$), as well as in both fertilized (R^2 = 0.90, df = 4, $P < 0.004$) and unfertilized (R^2 = 0.89, df = 4, $P < 0.005$) enclosures without predators (Fig. 5).

Nutrient Effects

Nutrient addition in 1992 increased mean TP to 17–21 μg·L^{-1} (18.3 ± 2.5, mean ± SD) in nutrient-addition enclosures, compared with 4–7 μg·L^{-1} (6.6 ± 0.8) in reference enclosures. Standing stocks of algae (measured as

TABLE 2. Repeated measures two-way analysis of variance for log-transformed densities of *Polyarthra dolichoptera* and *Keratella quadrata* from enclosures in 1992. The two treatments were presence or absence of the predator *Hesperodiaptomus arcticus* and addition or no addition of fertilizer.

Test	Source	df	MS	*P*
Polyarthra dolichoptera	Treatments			
	Hesperodiaptomus	1	25.8	0.0001
	Nutrient addition	1	0.22	0.28
	Interaction	1	0.20	0.30
	Error	8	0.16	
Keratella quadrata	Treatments			
	Hesperodiaptomus	1	3.87	0.006
	Nutrient addition	1	6.91	0.02
	Interaction	1	0.05	0.77
	Error	8	0.50	

chl *a*) increased significantly (repeated measures two-way analysis of variance, $F = 136.39$, df = 1.8, $P < 0.0001$) in the fertilized enclosures (Fig. 6). Differences in chl *a* between reference and nutrient-addition enclosures were greatest (fourfold) 14 d after the start of the experiment and then steadily declined in the nutrient-addition treatments until on the last day (35) there was only a marginal difference between treatments (Fig. 6).

Nutrient addition increased rotifer densities (Fig. 5). Densities of *K. quadrata* increased significantly in the fertilized enclosures (Table 2; Fig. 5). *Keratella quadrata* increased approximately one order of magnitude in response to nutrient additions in both enclosures with or without predators (Fig. 5). Mean densities of *P. dolichoptera* increased by an order of magnitude from day 23 to the end of the experiment in the nutrient addition enclosures without predators (Fig. 5), but the overall treatment effect was not statistically significant (Table 2). A similar but much smaller increase in *P. dolichoptera* was also observed in the nutrient-addition enclosures with predators (Fig. 5).

Geographic Distribution

In the 69 Canadian Rocky Mountain lakes investigated the proportion of lakes containing *Keratella* or *Polyarthra* decreased as the density of *Hesperodiaptomus* increased (Fig. 7). At low *Hesperodiaptomus* densities (<0.01 individuals·L^{-1}) *Polyarthra* occurred more frequently than *Keratella*. When densities of *Hesperodiaptomus* were high (>1 individual·L^{-1}) both rotifers occurred less frequently, but *Keratella* was the more common of the two (Fig. 7).

Logistic regression models for both rotifer genera predict that the probability of rotifers occurring decreases with increasing densities of *Hesperodiaptomus* (Fig. 8). Parameters for the model (*a* and *b* in Equation (1)) were significant for both rotifer species (Table 3). At *Hesperodiaptomus* densities >0.3 individuals·L^{-1} *Keratella* has a greater chance of occurring than *Polyarthra*, and at densities <0.3 individuals·L^{-1} *Polyarthra* has a higher chance.

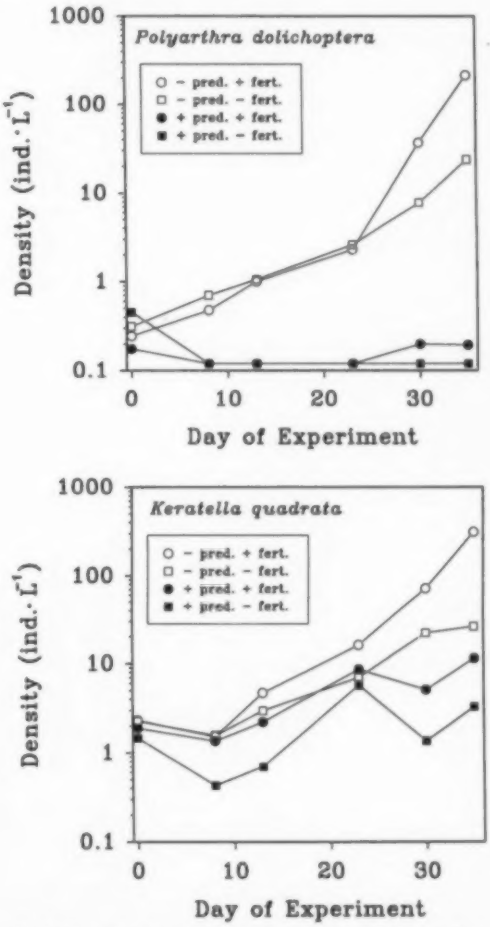

FIG. 5. Mean densities of the dominant rotifers *Polyarthra dolichoptera* and *Keratella quadrata* in enclosures with or without the predator *Hesperodiaptomus arcticus* or fertilizer for 1992.

Discussion

Predation by invertebrates can regulate rotifer populations in alpine lakes. Rotifer abundance was significantly reduced in the enclosures containing *H. arcticus* regardless of nutrient conditions, and the distributions of both *Keratella* and *Polyarthra* in 69 Canadian Rocky Mountain lakes were negatively correlated with *Hesperodiaptomus*. This negative relation with *Hesperodiaptomus* also applies to other rotifer genera in Rocky Mountain lakes (Anderson 1977, 1980). In contrast, studies from other systems have found that predation by *Chaoborus* (Havens 1990; Yan et al.

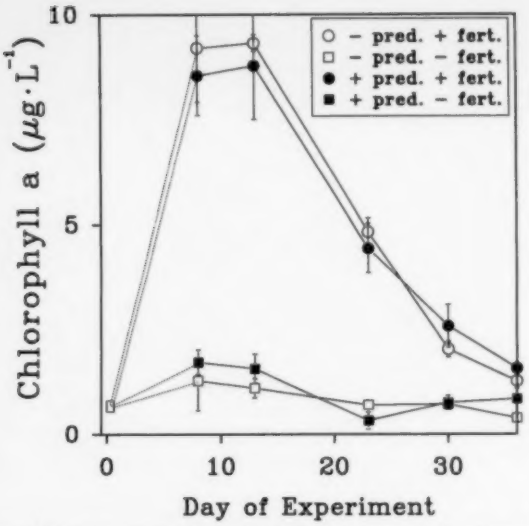

FIG. 6. Mean concentrations of chlorophyll *a* ($\mu g \cdot L^{-1}$) estimated by HPLC for enclosures with or without the predator *Hesperodiaptomus arcticus* or fertilizer for 1992. Day 0 represents lake concentrations and not means from enclosures. Error bars represent ±1 SE.

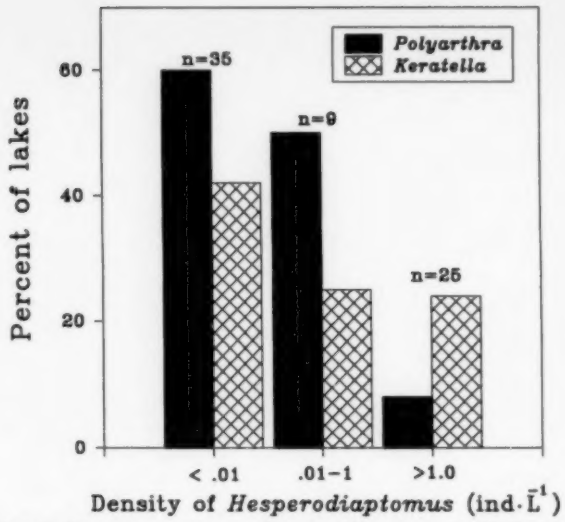

FIG. 7. Percent occurrence of two rotifer genera in 69 Canadian Rocky Mountain lakes with low to high densities of *Hesperodiaptomus*.

1991) or copepods (McQueen 1969; Neill 1984) does not control rotifer populations.

Invertebrate predators may be particularly effective in alpine lakes where low algal standing crop and cold water combine to reduce rotifer population growth. The high intrinsic growth rate of rotifers may allow them to outstrip predatory regulation in naturally acidic eutrophic lakes (Havens 1990), mesotrophic acidified fishless lakes (Yan et al. 1991), and oligotrophic montane lakes (Neill 1984). In alpine lakes, nutrient inputs and algal abundance are very low and rotifer growth may be food limited. Low reproductive rates may facilitate predatory regulation by *Hesperodiaptomus*. However, even though experimental nutrient additions (N and P) produced significant increases in chl *a* and rotifer abundance (*Keratella* only), predation from *H. arcticus* elicited a strong response for both rotifer species with or without nutrients (predation × nutrient interaction term was nonsignificant, Table 2). Future experiments will test whether higher nutrient levels, a longer experimental duration, or increased water temperatures may allow rotifer production to significantly surpass predator consumption.

Predatory regulation of rotifers in Rocky Mountain lakes may be a function of temperature. Snowflake Lake and most of the lakes from our survey have a short ice-free season and low midsummer surface water temperatures, 6–12°C (Anderson 1974; Lamontagne 1993). Edmondson (1965) reported that egg development times for *Polyarthra vulgaris* and *K. quadrata* had a Q_{10} of 0.49 and 0.45, respectively. This means that for a 10°C increase in temperature the time required for an egg to develop is reduced by almost a half. Lower reproductive rates of rotifers in alpine lakes may enable predators to significantly deplete their populations. Therefore, regulation of rotifers by *Hesperodiaptomus* predation may be facilitated through abiotic factors (low temperature regime). Community level experiments where predators, temperature, and food can be varied independently are needed to test the efficiency of these variables.

Daphnia pulex densities in our enclosure experiments were always below 0.1 individuals·L^{-1}, therefore, we saw no evidence of the regulation of rotifers through competition with *D. pulex*. Large *Daphnia* can suppress rotifer populations through both exploitative competition of similar food niches and interference competition at densities > 1 individual·L^{-1} (Gilbert 1988). Interference competition occurs when rotifers are swept into the branchial chamber of *Daphnia* where they may be ingested, rejected in a damaged condition, or have eggs detached (Gilbert and Stemberger 1985). Our experiments were done immediately after ice-out during a period when *Daphnia* were at low densities. Increased densities of *Daphnia* later in the season in Snowflake Lake did correspond to lower densities of rotifers, especially *Keratella*. This negative correlation may have been due to competition. The co-occurrence of density maxima for *Polyarthra* and *Daphnia* in 1992 indicates that these species may be able to coexist. Small rotifers (such as the dominant species in Snowflake Lake) may be better able to coexist with large *Daphnia* because they can reproduce at lower food levels than larger rotifer species (Stemberger and Gilbert 1985; Gilbert 1988).

We hypothesize, however, that *Hesperodiaptomus* predation is a more important determinant of rotifer populations in alpine lakes than competition from *Daphnia*. First, adult *Hesperodiaptomus* are present year-round in some Rocky Mountain lakes (Anderson 1974; A.J. Paul and D.W. Schindler, unpublished data) or for much of the ice-free season in others (Anderson 1967, 1974). Therefore, rotifers are subject to predation throughout the year or at least most of the ice-free season. Furthermore, *Daphnia* were abundant (> 1 individual·L^{-1}) in Snowflake Lake only during the latter half of the ice-free season, providing a substantial time period for rotifer growth in the absence of competition. Our results indicate that rotifers do reach high densities during periods of low *Daphnia* abundance (Fig. 2). Second, increased densities of *Hesperodiaptomus* were significantly related to the absence of *Keratella* and *Polyarthra* in 69 lakes (Table 3;

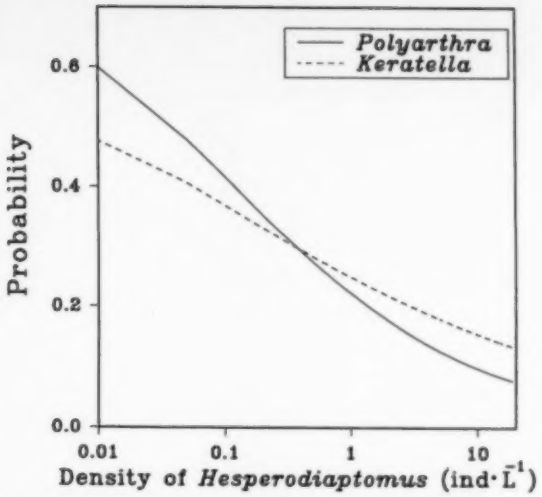

FIG. 8. Probability of occurrence for two rotifer genera in mountain lakes as a function of *Hesperodiaptomus* density using logistic regression analysis. Logistic equation parameters (*a* and *b* in Equation (1) were estimated from the raw values summarized in Fig. 7. The range in density of *Hesperodiaptomus* represents the observed density range from the 69 Canadian Rocky Mountain lakes.

Fig. 7 and 8); however, Anderson (1980) did not find any clear relation between cladoceran and rotifer populations from an empirical analysis of 320 lakes in the Canadian Rocky Mountains. Third, the number of new rotifer genera in Snowflake Lake has increased since fish stocking, even though *D. pulex* (but not *H. arcticus*) had returned to the lake by 1974. Finally, *H. arcticus* is the most common planktonic species in alpine lakes of the Canadian Rocky Mountains (Anderson 1971) and has been shown to strongly reduce rotifer populations (Fig. 4 and 5). These predictions and observations are consistent with the theory that the importance of predation and competition is related to abiotic conditions (Menge and Sutherland 1987; Arnott and Vanni 1993). Arnott and Vanni (1993) proposed that, in high-stress environments (e.g., extreme temperatures in alpine lakes), large herbivores are reduced in abundance and their importance in regulating smaller zooplankton diminishes while the importance of invertebrate predators increases.

Planktonic rotifers have several defences against predation including morphological, behavioral, physiological, and reproductive characteristics (Stemberger and Gilbert 1987). *Keratella* have rigid armoured loricas that could protect them from both capture and ingestion by copepods (Stemberger and Gilbert 1987). In contrast, *Polyarthra* are unarmoured but capable of rapid movements in response to a predator, thus avoiding predation by active escape (Gilbert 1980, 1985).

Our results indicate that *Keratella* may be better able to withstand *Hesperodiaptomus* predation than *Polyarthra*, even though both are of similar sizes. One prey species may be selected over another if it is "easier" to catch, if handling time for the predator is less, or if it is easier to ingest. The armoured lorica of *Keratella* likely decreases the probability of the predator successfully capturing or ingesting an individual. Other feeding experiments (Anderson 1970a) also showed that the soft-bodied rotifer *Synchaeta* was

TABLE 3. Logistic regression estimates and χ^2-statistics for the presence or absence of *Keratella* and *Polyarthra* as a function of $\log_{10}$-transformed densities of *Hesperodiaptomus*. The data are from 69 lakes in the Canadian Rocky Mountains. Parameters *a* and *b* refer to intercept and slope, respectively, in Equation (1).

Test	Parameter	Estimate	χ^2	*P*
Polyarthra	*a*	−1.21	6.58	0.01
	b	−0.95	12.36	0.0004
Keratella	*a*	−1.10	6.57	0.01
	b	−0.59	5.69	0.02

selected by *Hesperodiaptomus* over *Kellicottia*, a genus that has a spined lorica. Furthermore, *H. arcticus* predation in arctic ponds indicates that *D. pulex* with short tail spines are more susceptible to predation than genotypes with longer spines (Wilson and Hebert 1993). Significant reductions of *Keratella* by *Hesperodiaptomus* in 1992, although relatively unaffected in 1991, may be explained by higher predator densities and corresponding prey shortages. We conclude that *Hesperodiaptomus* is able to regulate abundance and distribution of both genera of rotifers through predation, but *Keratella* is better suited to withstand copepod predation owing to its armoured lorica.

The different responses of *Keratella* and *Polyarthra* to nutrient addition might be explained by their relative investments in defence. The cost of having a spined hard lorica may be an increase in threshold food requirements (Stemberger and Gilbert 1985, 1987). Therefore, *Keratella* may have responded more strongly to nutrient addition because limitation by food was greater owing to investments in predator defence. This hypothesis is supported from our model of distributional data. When predators are either rare or absent, *Polyarthra* may be more likely to occur than *Keratella* because it is better able to utilize food resources for reproduction. As predator density increases, *Keratella* begins to benefit from its investment in defence and its probability of occurrence surpasses that of *Polyarthra*. Further studies addressing costs and benefits of investments in defence are needed to substantiate the above hypotheses.

Elimination of *Hesperodiaptomus* in lakes by stocking with trout and char (Anderson 1972; Donald 1987) should change zooplankton community composition by allowing the colonization (or increase in abundance) of rotifers. The recolonization of a lake by *Hesperodiaptomus* could markedly decrease rotifer abundances and possibly exclude them. It seems unlikely that this relation would change with increased nutrient loads alone. We hypothesize that warmer temperatures may weaken the ability of *Hesperodiaptomus* to limit rotifers.

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Microbial Activity in Acidified and Limed Humic Lakes

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To test the hypothesis that acidification negatively affects microbial processes in water and sediment, five acidified (pH of surface water 5.2 ± 0.3) and five limed (pH 6.9 ± 0.2) humic (water colour 91 ± 15 and 77 ± 28 mg Pt/L, respectively) lakes in southern Sweden were studied. Sediment pH of the acidified lakes was significantly lower than in limed lakes down to a sediment depth of at least 3 cm. In spite of this, there was no difference between acid and limed lakes with respect to bacterial abundance in the sediment, sediment oxygen uptake, or utilization of amino acids by sediment bacteria. Similarly, there was no difference in biological water column parameters, i.e., chlorophyll *a*, gross and net oxygen production, respiration, bacterial abundance, and the utilization of amino acids by pelagic bacteria. Assuming that the restoration of pH by liming also restores pre-acidification conditions of microbial life, this study suggests that the level of acidification typical for most areas does not influence microbial activity negatively.

En vue de vérifier l'hypothèse voulant que l'acidification exerce un effet négatif sur les processus microbiens dans l'eau et les sédiments, on a étudié cinq lacs acidifiés (pH de l'eau de surface de 5,2 ± 0,3) et cinq lacs chaulés (pH de 6,9 ± 0,2) et humifères (coloration de l'eau de 91 ± 15 et de 77 ± 28 mg Pt/L, respectivement) du sud de la Suède. Le pH du sédiment des lacs acidifiés était significativement plus faible que celui des lacs chaulés jusqu'à une profondeur de sédiment d'au moins 3 cm. Malgré cela, il n'y avait aucune différence entre les lacs acidifiés et les lacs chaulés quant à l'abondance des bactéries dans les sédiments, la captation de l'oxygène dans les sédiments ou l'utilisation des acides aminés par les bactéries des sédiments. De même, il n'y avait aucune différence dans les paramètres biologiques de la colonne d'eau, c'est-à-dire, la chlorophylle *a*, la production brute et nette d'oxygène, la respiration, l'abondance des bactéries et l'utilisation des acides aminés par les bactéries pélagiques. Si l'on suppose que le rétablissement du pH par chaulage rétablit également la vie microbienne qui existait avant l'acidification, la présente étude laisse croire que le degré d'acidification caractéristique de la plupart des endroits n'influe pas de manière négative sur l'activité microbienne.

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Numerous investigations have been performed to assess possible effects of acidification on microbial activity in lakes. Reduced activity would decrease biogeochemical cycling of carbon and nutrients (Grahn et al. 1974) and microbial alkalinity generation (Kelly et al. 1982; Cook et al. 1986). Several studies indicate that acidification affects microbial activity negatively (e.g., Bick and Drews 1973; McKinley and Vestal 1982; Rao and Dutka 1983); other studies suggest no effect (e.g., Kollig and Hall 1982; Kelly et al. 1984; Gahnström and Andersson 1985; Schindler et al. 1985) or inconsistent negative effects (Andersson and Olsson 1985; Carpenter et al. 1983; Arvola et al. 1986). In a review of microbiological lake acidification research, Bell and Tranvik (1993) noted that negative effects of acidification are commonly detected in studies involving experimental acidification, some isolated part of a lake ecosystem, and/or highly disturbed experimental systems, such as sediment slurries. Experimental acidification often involves an abrupt initial acid shock, that has no counterpart in acidification of natural waters. Possibly, the commonly reported negative effects of acidification on microbes do not occur, or occur only to a minor extent in the natural environment, where anthropogenic acidification appears gradually. Consequently, in experiments involving complex, relatively undisturbed treatments such as lake mesocosms or whole lakes, there is a much lower incidence of documented negative effects of acidification, while no effect or a combination of no and negative effects are commonly reported in these studies (Bell and Tranvik 1993). Thus, the extensive evidence for negative effects of acidification on microbial activity may be biased, as it is largely derived from systems with reduced complexity (e.g., laboratory microcosms), while systems more representative of natural lakes (e.g., whole lake acidification experiments) often indicate no such effects (Bell and Tranvik 1993). Among the reports of negative effects of acidification in such "undisturbed" systems, several are based on comparisons of only two or three localities with different pH (Burnison et al. 1986; Hoeniger 1986; Leuven and Wolfs 1988; Mills and Herlihy 1985; Wassel and Mills 1983), sometimes with incomplete documentation of differences among the systems other than those related to acidification. In such studies, there is a possibility that the results are due to other properties of the studied lakes. Thus, we consider it still an open question whether or not acidification retards microbial activity in lakes.

Here, we present a survey of acidified humic lakes, some of which have been subject to liming as a means of restoring pH. Thus, they fall into two distinct categories in terms of pH and alkalinity, governed by the progress of an ongoing

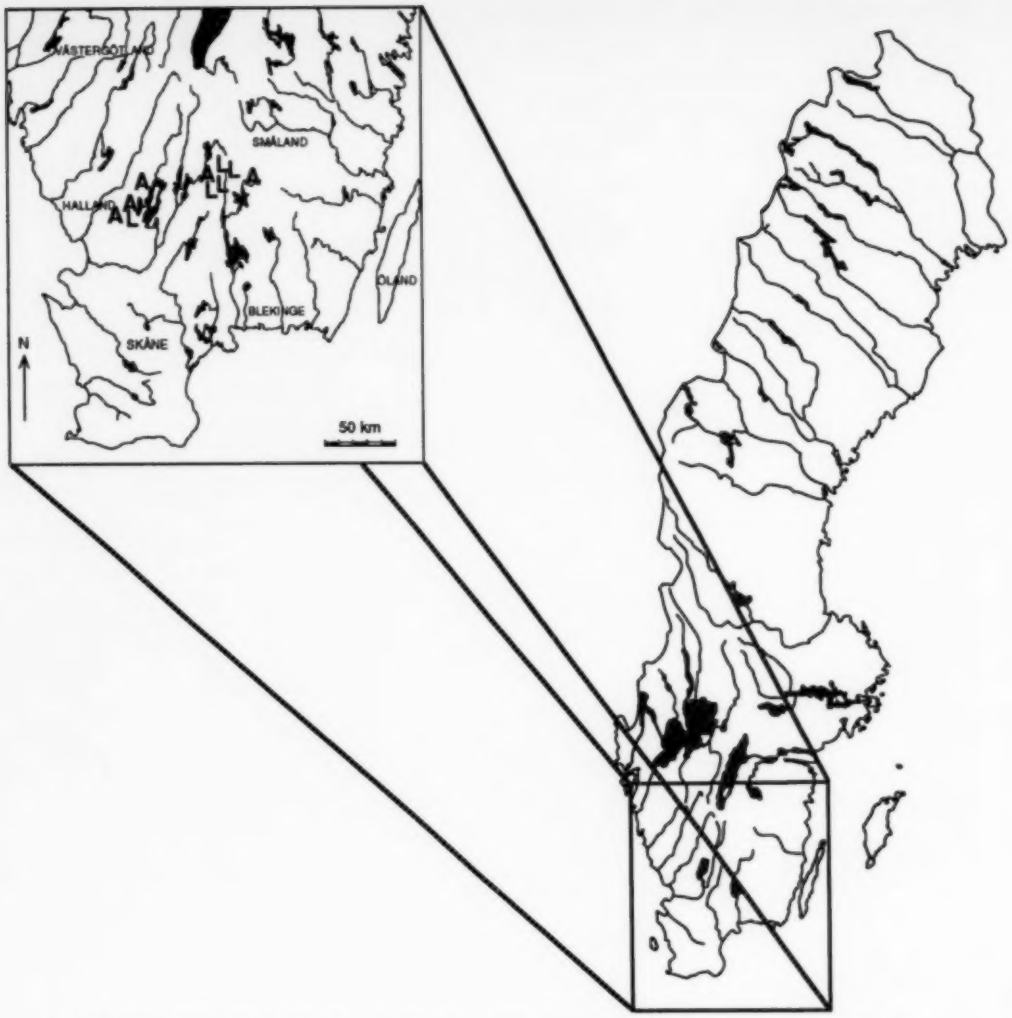

FIG. 1. Map of Sweden, indicating the location of the investigated acid (A) and limed (L) lakes.

extensive liming program in different parts of the study region. Except for the absence or presence of $CaCO_3$ due to liming activities, the group of lakes is very homogeneous. The differing acidity of the lakes is not a consequence of variations in geology of watersheds, or environmental gradients such as distance from a source of acid pollution, that may be correlated with other types of contaminants (e.g., heavy metals). Hence, we present a survey involving several replicates of either acid or circumneutral (limed) lakes, representative for the extent of acidification typical for large regions of Fennoscandia, and with minimal bias due to, for example, water chemistry differences other than those related to acidification and liming.

Materials and Methods

The survey included ten lakes in the southern coniferous forest region of Sweden (Fig. 1). All the lakes are within the regions of the South Swedish Highlands and the South Småland Archaean bedrock plain (Digerfeldt 1972), and are characterized by low buffering capacity and oligotrophic conditions. The lakes were selected using data bases of county administration and municipalities, to achieve a selection of lake as homogeneous as possible, except for the occurrence of liming activities. We chose to concentrate on moderately humic, oligotrophic lakes, as this is a dominating lake type in regions susceptible to acidification in Scandinavia. Physicochemical characteristics of the lakes are summarized in Tables 1–3. Temperature in the surface water ranged from 9.4–21.3°C during the study, and differed by at most 2.3°C between lakes within any of the four sampling occasions.

Samples were taken in all lakes during each of four 3-d periods in August and September 1990. Integrated water samples of 10 L were taken from 0–2 m depth. Replicate (n = 5) intact sediment cores (in perspex tubes of 4.4 cm diameter and 25 cm total length, length of sediment core 5–10 cm) were retrieved from each lake by a tube corer at

TABLE 1. Geographic coordinates according to the Swedish Meteorological and Hydrological Institute (1983) and ranges of pH, alkalinity, and water colour for the study lakes during the sampling period.

Lake	Coordinates	pH	Alkalinity (μeq/L)	Colour (mg Pt/L)
	Limed lakes			
Fersjön	X633883 Y143286	6.8–7.0	384–460	110–120
Gyslättasjön	X633209 Y141991	6.9–7.2	420–450	50–60
Stora Svansjön	X630533 Y135177	6.5–7.0	206–246	80–110
Stora Vällingen	X634102 Y142327	6.9–7.2	340–822	65–80
Stråken	X632688 Y142513	6.7–6.9	204–224	40–50
	Acid lakes			
Gransjön	X633526 Y143368	4.7–4.8	0	80–110
Harasjön	X632216 Y136456	5.3–5.4	8–25	70–80
Skärshultsjön	X633738 Y142203	5.6–5.7	26–30	80–90
Stora Lången	X630682 Y135214	5.3–5.6	14–32	80–110
Svartesjön	X631266 Y133969	4.9–5.1	0	90–120

TABLE 2. Physicochemical characteristics of acid and limed lakes (two left columns) and summary of effects according to ANOVA with repeated measures (three right columns). Values for physicochemical characteristics are means ± SD for all measurements (four sampling occasions in each of five lakes of each category, except for nutrients where there were only two sampling occasions). Values for ANOVA factors are probabilities. The null hypothesis is that there is no effect on the measured parameters of lake category (acid vs. limed) or time of sampling.

	Lake type		Factor		
Parameter	Acid	Limed	Treatment (lake type)	Repeated measure (time)	Interaction (lake type × time)
pH	5.2±0.3	6.9±0.2	0.0001	0.245	0.003
Alkalinity (mequiv./L)	0.01±0.01	0.37±0.18	0.0008	0.276	0.295
Conductivity (mS/m)	5.6±0.6	7.5±1.3	0.022	0.836	0.421
Water colour (mg Pt/L)	91±15	77±28	0.373	0.293	0.385
TOC (mg/L)	9.8±3.1	12.1±2.3	0.183	0.059	0.773
NO_3-N + NO_2-N (μg/L)	19.7±6.9	48.9±61.3	0.246	0.557	0.868
NH_4-N (μg/L)	14.0±13.4	14.7±12.1	0.898	0.065	0.947
Kjeldahl-N (mg/L)	0.50±0.08	0.57±0.06	0.053	0.034	0.601
PO_4-P (μg/L)	1.7±0.08	1.9±0.9	0.242	0.0003	0.999
Total P (μg/L)	13.7±2.4	15.7±4.1	0.198	0.014	0.063

a depth of ca 3 m. All incubations and fixation of subsamples were initiated on the day of sampling.

Alkalinity, pH, and conductivity were determined according to Swedish Standards Institution (1991). Alkalinity was measured by titration to pH 5.4 with hydrochloric acid; pH of water and sediment was determined potentiometrically using a combination electrode. Measurements were made directly in wet sediment after sectioning the sediment core. Water colour (mg Pt/L), a simple measure of humic content of water, was measured on Whatman GF/C filtered water with a Hellige colour comparator.

Samples for total organic carbon (TOC) were kept frozen in precombusted (500°C, overnight) glass vials with acid-rinsed, teflon-lined screw caps. Organic carbon of the rethawed samples was analyzed with a Shimadzu TOC 5000 total carbon analyzer, which uses platinum-catalyzed combustion at 680°C and subsequent infrared detection of CO_2. Prior to analysis, samples were acidified (pH 2) with HCl, and inorganic carbon was purged with CO_2-free air.

Nutrients were analyzed on a Technicon Autoanalyzer II according to Swedish Standards Institution (1991). Phosphate phosphorus was determined as molybdate reactive phosphorus (MRP) according to Murphy and Riley (1962). Total phosphorus was determined as MRP after autoclave digestion with peroxodisulphate. Nitrate and nitrite were analyzed according to Wood et al. (1967), ammonium according to Chaney and Marbach (1962), and organic nitrogen by the Kjeldahl digestion method.

Dry weight of sediment was measured after drying to constant weight at 65°C, and loss on ignition was determined after 2 h at 550°C.

Samples for enumeration of water-column bacteria were fixed with buffered, prefiltered (<0.2 μm) formaldehyde (2% final concentration). To count sediment bacteria

TABLE 3. Sediment characteristics of acid and limed lakes. Values are means for five acid and five limed lakes ± SD, measured on one occasion. The *p* values are derived from Mann–Whitney *U*-test of the null hypothesis that there is no difference between acid and limed lakes. Probabilities according to two-failed test, except for pH values, where a directed alternative hypothesis was meaningful (lower pH in acid lakes).

Parameter	Lake type		*p*
	Acid	Limed	
	pH		
Sediment/water interface	5.3±0.3	6.6±0.3	0.004
0.5 cm	5.4±0.4	6.5±0.4	0.004
1 cm	5.6±0.6	6.5±0.4	0.008
3 cm	6.3±0.6	6.9±0.4	0.048
	% water content		
0–1 cm	94.7±5.3	93.9±1.8	0.917
1–3 cm	91.6±2.0	86.0±7.3	0.096
	% loss on ignition		
0–1 cm	44.1±11.5	36.4±11.1	0.420
1–3 cm	42.9±13.0	32.4±12.9	0.420

1-cm-deep cores, representing 1 mL of sample, were carefully retrieved from undisturbed sediment cores with a cut-off plastic syringe. The sample was mixed with 50 mL of filtered (0.2 μm) lake water and fixed with formaldehyde, as above. Bacteria were counted by epifluorescence microscopy after staining with DAPI (Porter and Feig 1980). For counts of sediment bacteria, samples were diluted with filtered sodium pyrophosphate (0.2 μm, final concentration, 0.01 M), and sonicated to make the bacteria detach from sediment particles (Schallenberg et al. 1989). Sonicated, diluted samples were stained and counted as for the water-column samples.

Chlorophyll *a* was measured spectrophotometrically on methanol extracts of algae collected from water samples on Whatman GF/C filters (Swedish Standards Institution 1991).

Plankton respiration and primary production were measured by the oxygen method. For each lake, nine 60-mL clear glass bottles with ground stoppers were filled with water from a 5-L plastic carboy using a siphon with a 150-μm net to remove larger and thus more rare zooplankton. To three randomly selected bottles, 0.5 mL each of manganese chloride and alkaline iodide solutions was immediately added. Two sets of triplicate bottles were placed in an incubator with fluorescent light, one set in a blackened box. Temperature was adjusted to approximately the in situ value of the lake water (±2°C). Bottles were incubated for 16 h. Titrations were made with an automatic potentiometic procedure according to Granéli and Granéli (1991). From mean values of oxygen in the three treatments (initial, light, and dark) respiration (*R*), net (NP) and gross (GP) oxygen production, and the respiratory quotient (GP/*R*) were calculated.

Sediment cores were incubated in a darkened water bath at approximately in situ temperature. Oxygen was measured in the water overlying the sediment initially and after 10–16 h, using the procedure described above except that 30-mL oxygen bottles were used.

In addition to O_2 respiration, the respiration of ^{14}C-amino acids to CO_2 was used as a measure of microbial acitivity. Replicate live and killed samples (with 0.5 mL of 2 M NaOH) of 5 mL of water or 1 mL of sediment mixed with 5 mL of water were incubated in test tubes with gas-tight silicon septa. All samples were amended with a ^{14}C-labeled amino acid mixture (Amersham CFB.25) at a final concentration of 3 μg of amino acid carbon/L. After about 4 h in the dark at in situ temperature ± 2°C, incubation was terminated by the addition of 0.5 mL of 2 M NaOH through the septum of each test tube. Respired $^{14}CO_2$ was purged by bubbling with air after acidification of samples (1 mL of 2 M HCl), and collected in Packard Carbosorb inorganic carbon absorber (Larsson et al. 1988), for subsequent quantification by liquid scintillation counting.

Differences in sediment characteristics between acid and limed lakes were analyzed by Mann–Whitney *U*-test. All parameters measured repeatedly over time in the lakes were analyzed for differences between acid and limed lakes by ANOVA with repeated measures.

Results

The selected lakes differed markedly in all physicochemical characteristics expected to be influenced by liming. Thus, pH, alkalinity, and conductivity were higher in lakes that had been treated with $CaCO_3$ (Table 2). Also in the sediments, liming affected pH down to a depth of at least 3 cm (Table 3). Other characteristics did not differ significantly among the lakes. Concentrations of ammonium, organic nitrogen (as indicated by Kjeldahl nitrogen values), phosphate phosphorus, and total phosphorus in the water column were very similar in the acid and limed lakes. The concentration of $NO_3 + NO_2$ was not significantly different, although the average concentration in limed lakes was more than twice that in acid lakes. This was primarily due to one of the limed lakes (Stora Vällingen) having a much higher concentration than the others (80–119 μg/L), and an unexpectedly high value on one sampling occasion for another limed lake (Fersjön, 186 μg/L; six times higher than the other estimate from this lake), possibly due to contamination of the sample. For total phosphorus and Kjeldahl nitrogen, there was a significant temporal variation but no difference between acid and limed lakes. Sediment characteristics were similar in acid and limed lakes as revealed by organic content (indicated by loss on ignition) and water content (Table 3).

All lakes were characterized by chlorophyll concentrations on the order of 10 μg/L, and bacterial numbers in the water column on the order of 2×10^9/L (Fig. 2). These estimates of microbial standing stocks did not reveal any differences between acid and limed lakes (Table 4).

Similar to the estimates of algal and bacterial standings stocks in the water column, estimates of microbial activity (oxygen metabolism (Fig. 3), respiration of amino acids (Fig. 4)) did not indicate any significant differences between acid and limed lakes (Table 4). Gross O_2 production, net O_2 production, and respiration were all significantly affected by sampling time (Fig. 3, Table 4). Because the amount of chlorophyll was not influenced by time of sampling, the effect on production and respiration was most likely a temperature effect. The respiratory quotient did not show any difference among sampling dates (Table 4). Mean values were always well above 1, indicating a net autotrophic system.

TABLE 4. Summary of effects according to ANOVA with repeated measures, testing the null hypothesis that there is no effect on the measured parameters of lake type (acid vs. limed) or time of sampling. Values are probabilities.

Parameter	Factor		
	Treatment (lake type)	Repeated measure (time)	Interaction (lake type × time)
Water			
Bacterial abundance	0.808	0.087	0.610
Chlorophyll *a* concentration	0.306	0.228	0.196
Gross production	0.608	0.0003	0.160
Net production	0.512	0.017	0.235
Respiration	0.690	0.0001	0.297
P/R ratio	0.590	0.333	0.241
Amino acid respiration	0.151	0.003	0.319
Sediment			
Bacterial abundance	0.946	0.055	0.873
Respiration	0.368	0.796	0.533
Amino acid respiration	0.474	0.010	0.317

In sediments, there was also a lack of differences between acidified and limed lakes, as illustrated by data on bacterial abundance in the upper centimetre, O_2 respiration, and respiration of amino acids (Fig. 5, Table 4).

Discussion

In this study, we have focused on microbial activities indicative of total biomass and total processing of organic matter, such as oxygen consumption. The observed absence of acidification effects on these parameters indicates that microbial activity is not retarded, either by a direct effect of low pH or owing to decreased availability of inorganic and organic nutrients originating from primary production in the lakes or from allochthonous sources. However, this does not exclude the possibility of effects on other aspects, e.g., the genetic composition of microbial communities, such as has repeatedly been reported for phytoplankton (e.g., Almer et al. 1978; Stenson et al. 1993), and to some extent for heterotrophic bacteria (Mills and Mallory 1987). Moreover, it does not contradict previous indications of negative effects of acidification on microbes in lakes subjected to more severe acidification than the Scandinavian lakes studied here (Kelly et al. 1984).

Our lake survey included moderately humic lakes, which is a dominating lake type in acidified regions of Scandinavia and North America. Previous acidification research has been focused to a large extent on lakes with low concentrations of humic matter (Andersson and Olsson 1985; Overrein et al. 1980). In humic lakes, heterotrophic bacterial production is supported by allochthonous organic substrates derived from terrestrial vascular plants to a greater extent than in clear water lakes (Tranvik 1988, 1989). Compared with autochthonously produced dissolved organic carbon of algal origin, such substrates are of higher molecular weight (Tranvik 1990), and their degradation is probably to a greater extent dependent on exoenzymatic depolymerization (Schoenberg et al. 1990). It has been suggested that microbial utilization of substrates that require the action of extracellular enzymes is more sensitive to low pH than the processing of substrates that can be transported into a buffered

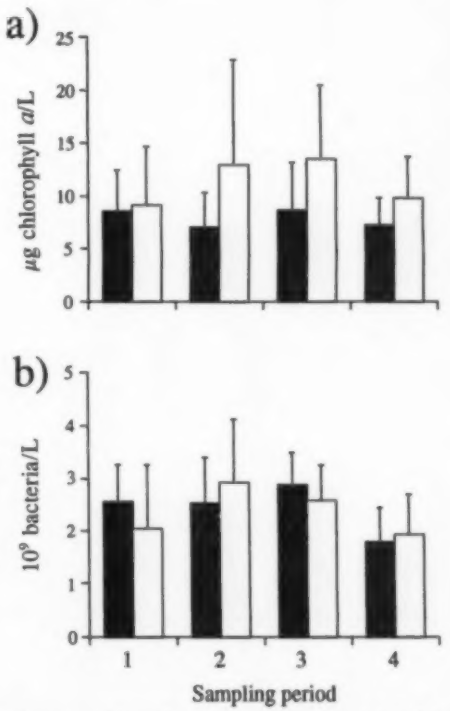

FIG. 2. Average chlorophyll *a* concentration (a) and bacterial abundance (b) in the water column of five acid (open bars) and five limed (solid bars) lakes. Error bars indicate standard deviation.

intracellular environment independently of exoenzymes (Benner et al. 1989). Accordingly, Schoenberg et al. (1990) showed that the degradation of vascular plant lignocellulose is retarded at low pH to a larger extent than the degradation of organic carbon from algae. Thus, environments where detritus derived from vascular plants is an important fraction of the microbial substrate, such as humic lakes, would be more sensitive to acidification than environments

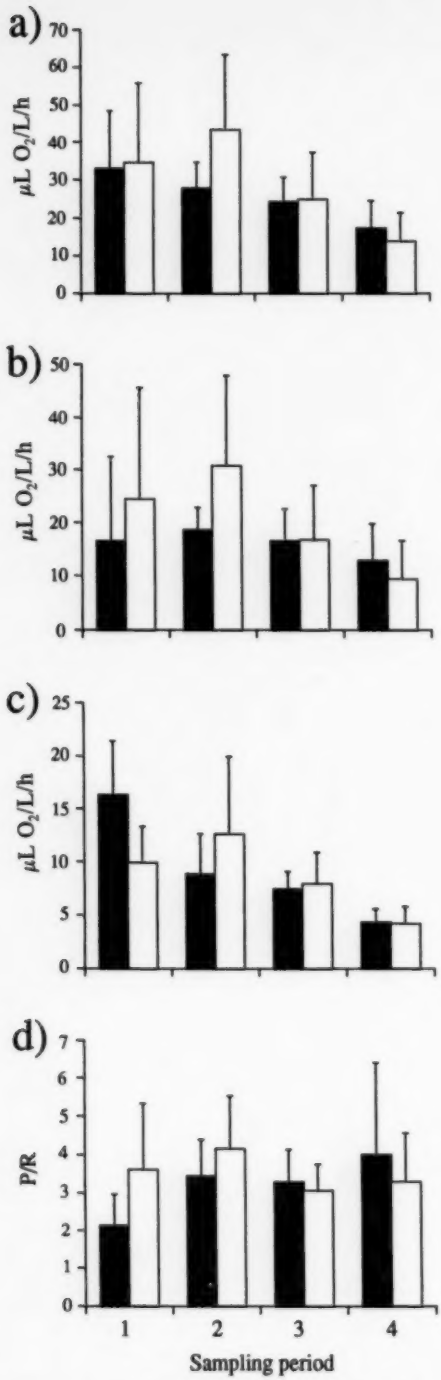

FIG. 3. Average gross production (a), net production (b), respiration (c), and *P/R* ratio (d) in the water column of five acid (open bars) and five limed (solid bars) lakes. Error bars indicate standard deviation.

where organic carbon of algal origin is the dominating bacterial substrate, such as clearwater lakes. In this study, we found no effect of acidification in humic lakes, although

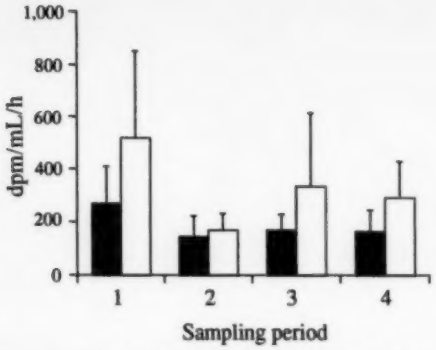

FIG. 4. Average amino acid respiration in the water column of five acid (open bars) and five limed (solid bars) lakes. Error bars indicate standard deviation.

their microbiota is possibly more sensitive than the microorganisms of several other types of lakes.

In previous mesocosm experiments we found little evidence for differences in microbial activities either in the water column or in the sediment among mesocosms that had been either acidified, limed, or left without manipulation (G. Gahnström, W. Granéli, and L. Tranvik, unpublished data). The only pronounced difference that was found among the treatments was decreased chlorophyll *a* concentration and oxygen consumption in limed mesocoms for one of the experiments, probably owing to an initial pH shock or coprecipitation of microorganisms and $CaCO_3$. Here, we corroborate the lack of consistent negative effects of low pH by demonstrating that acidified lakes do not differ in microbial activity from acidified lakes that had their pH restored by liming. In this investigation, we did not find a negative effect of liming on chlorophyll *a* and oxygen comsumption. The limed lakes included in this study were treated with a liming agent at a minimum of 1 yr before our study, while the negative effect of liming in mesocosms (G. Gahnström, W. Granéli, and L. Tranvik, unpublished data) and lakes (Gahnström 1988) was recorded weeks after liming. Hence, the lack of such effects in the lake survey does not exclude the fact that initial "liming shocks" occur in lakes.

To our knowledge, this study comprises, to date, the most homogeneous and well-characterized selection of lakes used in a comparative study of acidification effects on microbial activity. The study lakes are representative of Scandinavian lakes that are subject to acidification caused by the long-range dispersal of acids produced during fossil fuel combustion. They differed in pH owing to the liming of some of the lakes, but were similar in other ways. Thus, the observed absence of effects of acidification and liming can be applied to a wide geographic region, although significant effects may possibly be found in local areas with severe acidification, e.g., owing to mine drainage or location in the vicinity of industrial plants. Hence, our results do not contradict negative effects of acidification documented for such lakes. However, they may be more representative of lakes of wider geographic regions receiving acidic deposition due to long-range atmospheric dispersal. A conservative conclusion would be that the liming of acidified lakes does not cause any change in microbial activity that can be detected by our methods, given other sources of variation among the lakes. Assuming that the restoration of pH by liming also restores

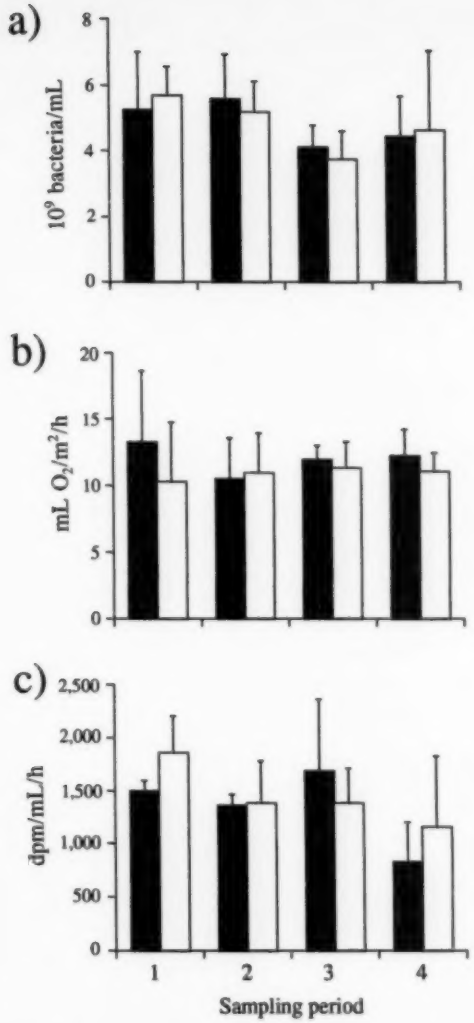

FIG. 5. Average bacterial abundance in the upper centimetre (a), O_2 respiration in sediment cores (b), and respiration of amino acids in the upper centimetre (c) of the sediment of five acid (open bars) and five limed (solid bars) lakes. Error bars indicate standard deviation.

pre-acidification conditions of microbial life, this study also suggests that the level of acidification studied here does not influence microbial activity negatively.

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Estimating the Number of Fish Landed from Their Total Weight and a Sample Average Weight

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Assessing the status of a commercially exploited fish stock usually involves fitting a model for the stock's dynamics to observations of the number of fish landed. Typically, the number of fish landed is estimated from the ratio of the total landed weight, which is known exactly, over the sample average weight of a fish. This paper examines how errors in the sample average weight are transformed asymmetrically into errors in the estimate of the numbers landed when samples consist of fixed numbers of fish. Two alternative estimators are developed and are shown, using Monte Carlo simulations, to be less biased than the standard estimator.

L'évaluation d'un stock de poisson qui fait l'objet d'une exploitation commerciale nécessite habituellement l'ajustement d'un modèle de la dynamique du stock aux observations portant sur le nombre de prises. De manière caractéristique, le nombre de prises est estimé à partir du rapport entre le poids total des prises, qui est connu de façon précise, et le poids moyen de contrôle d'un poisson. On examine ici comment les erreurs de poids moyen de contrôle sont transformées asymétriquement en erreurs de l'estimation du nombre de prises lorsque les échantillons comprennent des nombres fixes de poissons. On a élaboré deux autres estimateurs qui, a l'aide de simulations de Monte Carlo, se sont révélés moins biaisés que l'estimateur type.

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A basic task in fisheries research is to assess how fishing influences the stocks. Without a monitoring program to measure removals by man and trends in stock abundance, fisheries scientists and managers cannot discern whether harvest rates might be jeopardizing a fishery's long-run success. Although regulatory agencies often require fishermen to report the total weight of their landings, managers need additional information to assess accurately a stock's status. Fisheries agencies typically employ samplers to collect data on the biological characteristics of the fish landed, for example, maturity, average size, and age and sex frequency (Doubleday and Rivard 1983). Then the agencies' assessment scientists combine this supplementary information with the basic landings data and other data such as research surveys and attempt to reconstruct each stock's demographic history by fitting an age-structured population model to estimates of the numbers of fish removed each year from each age-class, the so-called catch-at-age data (Megrey 1989). These age-structured assessment techniques require accurate and reliable catch-at-age information.

Often estimates for catch-at-age are derived from a two-stage sampling design in which subsamples of fish are collected from a sample of the landings (Gulland 1966; FAO 1981; Caddy and Bazigos 1985). The following hypothetical example is more or less typical of the general scheme. A port sampler takes a sample of fish from the landings by a particular boat trip, weighs the sample, counts the fish in it, removes the material used for age determination (e.g., otoliths, scales, or bones), and reports all this information either directly or indirectly to an assessment scientist. For the total landings by this boat trip the scientist estimates the catch-at-age by expanding the sample age frequency by a "raising factor," equal to the ratio of the weight of the landings by the boat trip over the weight of the sample. He computes the quarterly catch-at-age for the port by simple addition of the catch-at-age estimates across those boat trips that were sampled with expansion for those that were not sampled. He calculates the quarterly catch-at-age for the entire stock by addition across ports and estimates the annual catch-at-age by addition across quarters. Usually the number of boat trips sampled within each port–quarter combination is small (1–5 trips), but the number of fish sampled from a boat trip is reasonably large (20–100 fish).

The procedure for expanding a sample age frequency is algebraically equivalent to multiplying the sample proportions-at-age by an estimate of the total number of fish landed: $\hat{N}_a = p_a \hat{N}$ where $\hat{N} = W/\bar{w}$, $\hat{N}_a$ is the estimated total number of fish in age-class a, p_a is the sample proportion of fish of age-class a, $\hat{N}$ is the estimated total number of fish landed, W is the total weight of the landings, and $\bar{w}$ is the average weight of the fish sampled. Usually $\bar{w}$ is calculated as the ratio of the sample weight over the number of fish in the sample, and the weights of individual fish are not measured. Quinn et al. (1983), Gavaris and Gavaris (1983), Sen (1986), and the Inter-American Tropical Tuna Commission (1991) all use these formulas, or variants of them, in their estimators for catch-at-age. Also, Westrheim (1967) suggests using similar formulas to expand data collected during research vessel surveys when large catches are subsampled.

Although it seems very reasonable to estimate the number of individuals in some collection by dividing the total weight of the collection by the average weight of an individual,

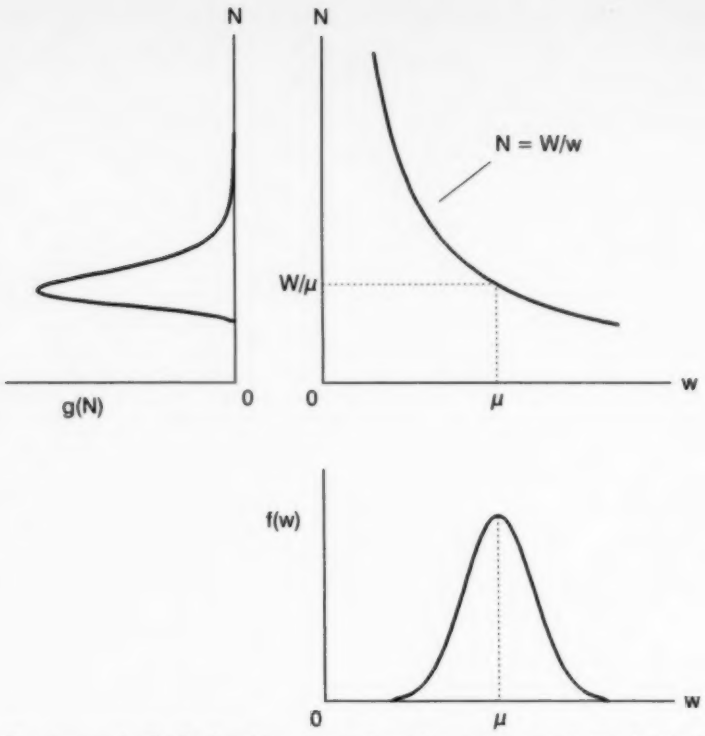

FIG. 1. The symmetric distribution for w is transformed to an asymmetric distribution for N. In this example, w is distributed as a truncated normal distribution (Table 1, A), where truncation occurs for values of $|w - \mu|$ greater than (σ).

unless the entire collection is measured, the average weight will not be known with complete certainty. In the next section, I show that measurement errors in the estimate of average weight are transformed asymmetrically to errors in the estimate of N. If the sample size is fixed, this produces estimates of N that are positively biased.

Theoretical Considerations

There are technical problems associated with obtaining a representative sample from a large collection of fish (Gulland 1966; Tomlinson 1971). Because it is generally impossible to enumerate the entire landings by a vessel, a sampling frame for selecting a random sample of fish is generally ill defined. Nevertheless, suppose samples of fish can be selected in some randomized manner that produces unbiased estimates of the average fish weight. If samples with a fixed number of fish are taken repeatedly from the collection and the sample average weights are tabulated, these averages will follow some distribution whose mean value will equal the average fish weight for the entire collection. Furthermore, the distribution will, with increasing sample size, tend towards a normal distribution (the central limit theorem). This result can be used to examine how errors in the sample average weight propagate errors in the estimate of the number of fish.

Suppose w is distributed as a positive random variate from a symmetrically truncated normal distribution. Define N to be the following nonlinear function of w: $N = h(w) = W/w$, $N \geq 1$. The function $h(w)$ defines a one-to-one transformation that tends to spread out large values of w and compress small values (Fig. 1).

The probability density functions for w and N can be used to examine the relationship between the average w and the average N. If $f(w)$ is the probability density function for w (Table 1, A), then the probability density function for N is given by

$$g(N) = \begin{cases} f(W/N)W/N^2 & \text{for } h(\mu + \tau\sigma) < N \\ & \quad < h(\mu - \tau\sigma) \\ 0 & \text{for elsewhere} \end{cases}$$

(Hogg and Craig 1970), where μ is the average value of w, σ is the standard deviation of w in the absence of truncation (as τ approaches infinity), and τ controls the points of truncation.

Now, define δ to be the relative bias of N:

$$\delta = \frac{[E(W/w) - W/\mu]}{(W/\mu)}.$$

Sigma (δ) is the relative difference between the average N, which is $E(W/w)$, and the function $h(w)$ evaluated at the average w, which is $h[E(w)]=W/\mu$. To examine the relationship between the moments of the two random variables w and N, I used numerical techniques and specific values for μ, σ, τ, and W, and found a reasonably simple relationship between δ and the coefficient of variation of w (Fig. 2). The coefficient of variation of w is given by

$$\mathrm{CV}(w) = \frac{\sigma_w}{\mu_w} = \frac{1}{\mu}\left[\int_{-\infty}^{\infty} [w - \mu]^2 \, f(w)\, dw\right]^{1/2}.$$

Note that because $f(w)$ is zero for extreme values of w if τ is finite, the standard deviation of w is less than σ and $CV(w)$ is less than σ/μ.

Sigma (δ) is a nonlinear function of $CV(w)$ (Fig. 2). If there is nonzero variability in w, then δ is greater than zero and the average value of N is greater than the transformed value of the average w, $E(N) > (W/\mu)$. This result also follows directly from Jensen's inequality, which states that if $h(w)$ is a convex function, then $E[h(w)] \geq h(E[w])$ (Bickel and Doksum 1977). The relationship between δ and $CV(w)$ implies that the ratio of the total weight of a collection of fish (W) over the sample average weight of a fish ($\bar{w}$) is a positively biased estimator of the number of fish in the collection (N).

The Taylor series expansion for $N = (W/w)$ provides another method for examining the relationship between the moments of w and the average N. Furthermore, the series expansion leads to an estimate of the bias associated with using $W/\bar{w}$ as an estimate for $E[N]$. The expansion for $N = (W/w)$ about the point $w = \mu$ can be written as $N = (W/\mu)[1 - (w/\mu - 1) + (w/\mu - 1)^2 - (w/\mu - 1)^3 + \ldots]$. This series converges provided $|w| < (2\mu)$. After applying the expectation operator to the above equation, the following formula for the average N can be derived: $E(N) = (W/\mu)[1 + E[(w - \mu)^2]/\mu^2 - E[(w - \mu)^3]/\mu^3 + \ldots]$. If w is symmetrically distributed, then the terms with odd powers are all zero. If w is also normally distributed, then the terms with even powers are simple functions of the coefficient of variation of w: $E[(w - \mu)^j]/\mu^j = (2i - 1)\cdots 5\cdot 3\cdot 1\cdot(\sigma/\mu)^{2i}$, for $j = 2i$, $i = 1, 2, 3, \ldots$, and the series is a function of $CV(w)$ alone. It does not depend separately on the mean and variance of w.

If w is approximately normally distributed, then from the above it follows that a second-order approximation for $E(N)$ is

$$(1)\quad E(N) \approx (W/\mu)[1 + CV(w)^2],$$

and a fourth-order approximation is

$$(2)\quad E(N) \approx (W/\mu)[1 + CV(w)^2 + 3CV(w)^4].$$

Values for δ based on these approximations correspond closely to the true relationship between δ and $CV(w)$ (Fig. 2).

New Estimators for the Number of Fish

If μ is the true average weight of an individual in a collection and W is the total weight of the collection, then the true number of individuals in the collection is given exactly by $N = W/\mu$. However, if N is estimated by the ratio of the total weight to the sample average weight $\bar{w}$, and the average is based on samples of fixed numbers of individuals, then Equation (1) indicates that $W/\bar{w}$ will on average be larger than W/μ by an amount approximately equal to $(W/\mu)CV(\bar{w})^2$. This amount can be removed from the estimator $W/\bar{w}$ to correct for its positive bias. Although the true values for μ and $CV(\bar{w})$ will not be known, estimates can be derived from the sample data.

Let $\hat{N}_1$ be the standard estimator for N:

$$(3)\quad \hat{N}_1 = W/\bar{w}.$$

Here are two alternative estimators, based on Equations (1) and (2):

$$(4)\quad \hat{N}_2 = \frac{(W/\bar{w})}{1 + \widehat{CV}(\bar{w})^2}$$

TABLE 1. Probability density functions used in the Monte Carlo tests. μ_w denotes the expected value of w and σ_w denotes the standard deviation of w.

(A) Truncated normal distribution

$$f(w) = \begin{cases} \dfrac{\varphi(w;\mu,\sigma)}{1 - 2\Phi(-\tau;\mu,\sigma)} & \text{for } \mu - \tau\sigma < w < \mu + \tau\sigma \\ 0 & \text{for elsewhere} \end{cases}$$

$$\varphi(w;\mu,\sigma) = [\sigma(2\pi)^{1/2}]^{-1}\exp\{-1/2[(w - \mu)/\sigma]^2\}$$

$$\Phi(\tau;\mu,\sigma) = \int_{-\infty}^{\tau} \frac{1}{\sigma(2\pi)^{1/2}}\exp[-1/2[(w - \mu)/\sigma]^2]\,dw$$

$\mu = 100.0$ $\sigma = 33.3$ $\tau = 3.0$
$\mu_w = 100.0$ $\sigma_w = 32.85$

(B) Uniform distribution

$$f(w) = \begin{cases} 0.005 & \text{for } 0 < w < 200 \\ 0 & \text{for elsewhere} \end{cases}$$

$\mu_w = 100.0$ $\sigma_w = 57.735$

(C) Right-skewed β-distribution

$$f(w) = \begin{cases} B(\alpha,\beta)^{-1}(w/200)^{\alpha-1}(1 - w/200)^{\beta-1} & \text{for } 0 < w < 200 \\ 0 & \text{for elsewhere} \end{cases}$$

$$B(\alpha,\beta) = \int_0^1 u^{\alpha-1}(1-u)^{\beta-1}\,du$$

$\alpha = 2.0$ $\beta = 5.0$
$\mu_w = 57.143$ $\sigma_w = 31.944$

(D) Left-skewed β-distribution

$f(w)$ as in (C) but with different parameter values.
$\alpha = 5.0$ $\beta = 2.0$
$\mu_w = 142.857$ $\sigma_w = 31.944$

(E) Mixture of two normal distributions

$f(w) = p\varphi(w;\mu_1,\sigma_1) + (1 - p)\varphi(w;\mu_2,\sigma_2)$
$\varphi(w;\mu,\sigma)$ as in (A).
$\mu_1 = 40.0$ $\sigma_1 = 10.0$ $p = 0.75$
$\mu_2 = 160.0$ $\sigma_2 = 40.0$
$\mu_w = 70.0$ $\sigma_w = 56.347$

(F) Log-normal distribution

$$f(w) = \begin{cases} (1/w)\varphi[\ln(w),\mu,\sigma] & \text{for } 0 < w \\ 0 & \text{for elsewhere} \end{cases}$$

$\varphi(w;\mu,\sigma)$ as in (A).
$\mu = 3.80045$ $\sigma = 1.26864$
$\mu_w = 100.0$ $\sigma_w = 200.0$

$$(5)\quad \hat{N}_3 = \frac{(W/\bar{w})}{1 + \widehat{CV}(\bar{w})^2 + 3\widehat{CV}(\bar{w})^4}.$$

In these last two formulae the quantity $\widehat{CV}(\bar{w})$ denotes the estimated coefficient of variation of $\bar{w}$, $\hat{\sigma}/(\hat{\mu}/\sqrt{n})$, which is given by

$$(6)\quad \widehat{CV}(\bar{w}) = \frac{1}{\bar{w}}\left[(1 - \Sigma w/W)\frac{\Sigma(w - \bar{w})^2}{n(n-1)}\right]^{1/2}$$

if the samples are simple random ones and are size n and drawn without replacement. The term $(1 - \Sigma w/W)$ in

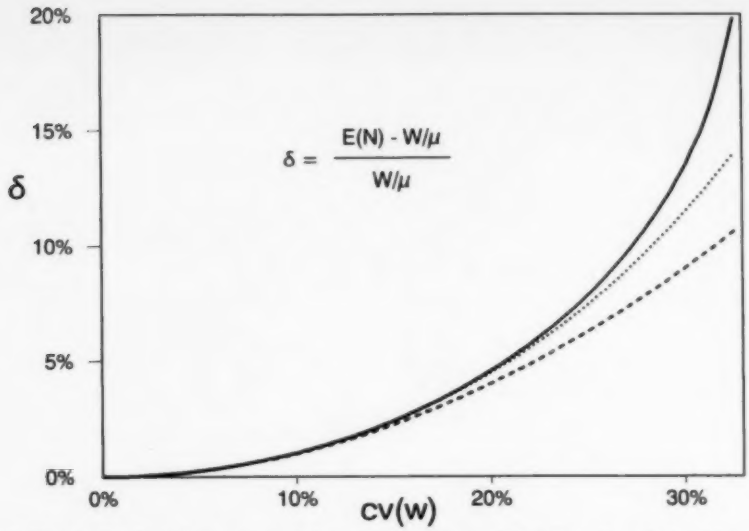

FIG. 2. If w is distributed as a truncated normal random variable, then the relative bias (δ) in the estimator $N = W/w$ is a nonlinear function of the coefficient of variation of w. The broken line represents the relative bias in an estimator based on the second order Taylor series approximation; the dotted line represents the relative bias in the estimator based on the fourth-order approximation. For this figure, values of $|w - \mu|$ greater than (3σ) were truncated. Slightly different curves result from other values for the truncation parameter.

Equation (6) is an estimate of the finite population correction factor $(1 - n/N)$ (Cochran 1977). Note that $\overline{\mathrm{CV}}(\bar{w})$ is zero if the entire population is sampled, and in this case all three estimators produce the correct value for N.

Estimated Variance of $\hat{N}$

The Taylor series expansion can also be used to derive the following approximate estimator for the variance ($\hat{V}$) of $\hat{N}$:

$$(7)\quad \hat{V}(\hat{N}) \approx [(W/\bar{w})\overline{\mathrm{CV}}(\bar{w})]^2.$$

This formula is equivalent to the variance estimator proposed by Quinn et al. (1983) and Gavaris and Gavaris (1983).

Monte Carlo Tests of the Estimators

To evaluate the performance of the three estimators $\hat{N}_1$, $\hat{N}_2$, and $\hat{N}_3$, given by Equations (3)–(5), I used Monte Carlo simulation techniques and the following algorithm.

(1) Generate random weights for a population consisting of $N = 1000$ individuals. Record the total weight.

(2) Randomly select without replacement a fixed number of individuals and for this sample calculate $\bar{w}$ and $\overline{\mathrm{CV}}(\bar{w})$. For each estimator, calculate the estimate of the total population size and calculate the residual error, $\hat{N} - N$.

(3) Repeat step (2) for a large number of trials.

(4) For each estimator calculate the average value for the estimates of N and calculate the root mean square error (the square root of the average squared residual).

(5) Repeat steps (2)–(4) for different fixed sample sizes.

(6) Repeat steps (1)–(5) for 10 realizations of the underlying distribution for weight.

I used fixed sample sizes of 2, 5, 10, 25, 50, 100, and 200 individuals, and varied the number of trials associated with each fixed sample size so that I always sampled a total of 200 000 individuals.

Note that there are two levels of randomization in the data. I used a "parental" population to produce a series of finite random populations, and then randomly selected samples from these particular realizations.

I used six different parental distributions (Table 1; Fig. 3) for generating the finite populations from which the samples were drawn: a truncated normal distribution (Fig. 3A); a uniform distribution (Fig. 3B); a right-skewed β-distribution (Fig. 3C); a left-skewed β-distribution (Fig. 3D); a right-skewed mixture of two normal distributions (Fig. 3E); and a log-normal distribution (Fig. 3F).

The weight–frequency distributions observed in a real fishery are likely to arise from much more complicated distribution functions than any of the six considered in the Monte Carlo tests. In many fisheries the landings are composed of a mixture of age-classes with the weight-at-age being more or less normally distributed. A mixture of normal distributions can take on a great variety of different shapes.

Monte Carlo Test Results

As a measure of the bias of each estimator ($\hat{N}_1$, $\hat{N}_2$, and $\hat{N}_3$), I calculated the mean (averaged over the 10 randomly generated populations) of the average estimates of N for each parental distribution (Fig. 3A–3F), for each fixed sample size (2, 5, 10, etc.), and for each estimator (Table 2, the rows labeled "Ave.").

As a measure of the accuracy (bias plus precision) of each estimator I calculated the mean (averaged over the 10 randomly generated populations) of the square root of the relative mean square error (root relative MSE): Root relative MSE = $\{\mathrm{ave}[\sum(\hat{N}/N - 1)^2]\}^{1/2}$, for each distribution, sample size, and estimator (Table 2).

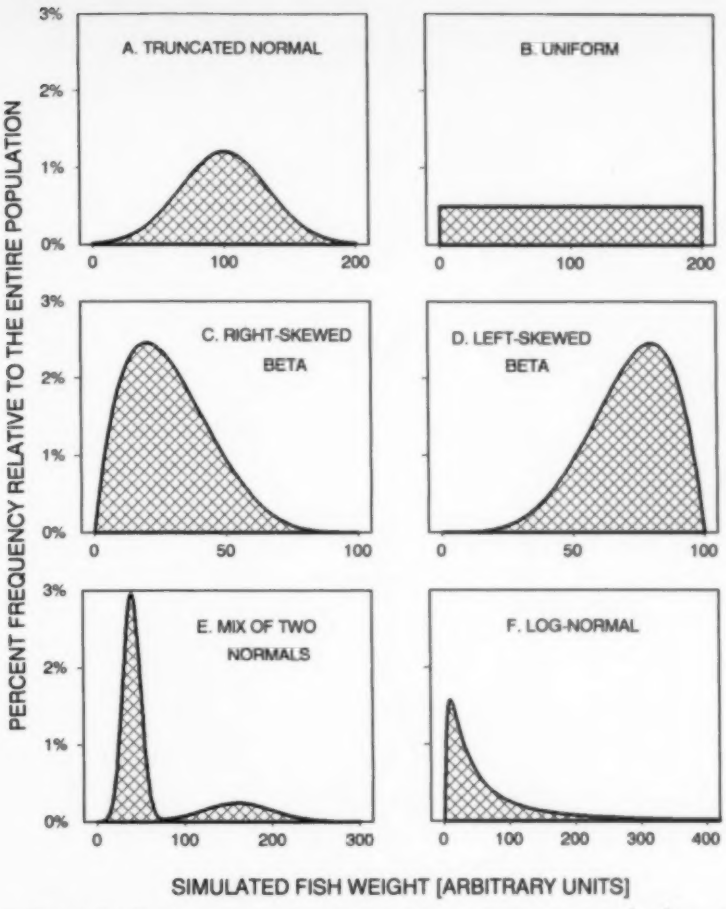

FIG. 3. Parent distributions used in the Monte Carlo testing of estimators $\hat{N}_1$, $\hat{N}_2$, and $\hat{N}_3$.

To measure the variability among the 10 random populations (as opposed to the variability due to randomly sampling from a single finite population) I calculated the standard deviations (taken over the 10 randomly generated populations) for each of the various estimates (Table 2, the rows labeled "SD"). In general, the variation in the results due to variability among the 10 populations was small relative to the variation due to sampling within a population.

For all six parental distributions the simple estimator $\hat{N}_1$ was positively biased with the bias rapidly decreasing as the sample size increased (Table 2). For the truncated normal distribution with a sample size of two the estimates $\hat{N}_1$ were, on average, about 6% too large, but they were essentially unbiased with sample sizes of 100 or more. The greatest bias occurred with the log-normal distribution (Table 2, F). With a sample size of two the estimates $\hat{N}_1$ average 2.5 times the true value, and even with a sample size of 200 they were about 1% too large.

The second-order estimator $\hat{N}_2$ was in all cases less biased than $\hat{N}_1$, and in most cases it was also more accurate, producing estimates with smaller mean square errors (Table 2). For some of the distributions the improvement in accuracy was substantial. For example, with the populations drawn from the uniform distribution (Table 2, B) and a sample size of two, the estimates $\hat{N}_1$ were on average about 40% too large but the estimates $\hat{N}_2$ were only 15% too large.

The fourth-order estimator $\hat{N}_3$ was always more accurate than $\hat{N}_1$ and was often slightly more accurate than $\hat{N}_2$ (Table 2). However, the estimates $\hat{N}_3$ were sometimes negatively biased. For example, with the populations from the right-skewed β-distribution (Table 2, C) and a sample size of two, the estimates $\hat{N}_3$ were on average 16% too small, whereas the estimates $\hat{N}_1$ and $\hat{N}_2$ were 22% and 7% too large.

Besides testing the bias and accuracy of the estimators for population size, I also examined the validity of the approximate variance estimator given by Equation (7). For each of the six parental distributions and for each of the fixed sample sizes, I calculated the mean (averaged over the 10 randomly generated populations) of the average estimated standard error for $\hat{N}_2$ (Table 3). I also calculated T values,

$$T = \frac{(\hat{N}_2 - N)}{[\hat{V}(\hat{N})]^{1/2}},$$

and tabulated the percentage of the estimates $\hat{N}_2$ that were within one, two, and three standard errors of the true N (Table 3).

TABLE 2. Monte Carlo evaluation of the bias and accuracy of three estimators for N. For all trials the true population size, N, was 1000 individuals. For each parental distribution (A–F) the average estimates (Ave.) are means over 10 randomly generated populations; the standard deviations (SD) measure the variability among the 10 populations.

Sample size	No. of trials		Estimated population size			Root relative MSE[a]		
			$\hat{N}_1$	$\hat{N}_2$	$\hat{N}_3$	$\hat{N}_1$	$\hat{N}_2$	$\hat{N}_3$
			(A) Truncated normal distribution					
2	100 000	Ave.	1066.3	1001.3	975.8	32.2	27.4	27.4
		SD	5.3	1.0	3.3	1.9	1.3	1.3
5	40 000	Ave.	1022.7	998.9	996.3	16.3	15.1	15.0
		SD	1.9	1.1	1.3	0.6	0.5	0.5
10	20 000	Ave.	1011.3	999.9	999.5	10.9	10.5	10.5
		SD	1.0	0.8	0.8	0.4	0.3	0.3
25	8 000	Ave.	1004.2	999.9	999.8	6.6	6.5	6.5
		SD	0.7	0.8	0.8	0.2	0.2	0.2
50	4 000	Ave.	1002.3	1000.2	1000.2	4.6	4.5	4.5
		SD	1.0	0.9	0.9	0.2	0.2	0.2
100	2 000	Ave.	1001.1	1000.1	1000.1	3.1	3.1	3.1
		SD	0.8	0.8	0.8	0.1	0.1	0.1
200	1 000	Ave.	1000.5	1000.0	1000.0	2.1	2.1	2.1
		SD	0.6	0.6	0.6	0.1	0.1	0.1
			(B) Uniform distribution					
2	100 000	Ave.	1412.3	1148.6	996.6	215.3	172.0	155.9
		SD	31.7	18.4	11.1	44.0	32.7	27.2
5	40 000	Ave.	1088.1	996.7	967.4	39.2	31.7	29.5
		SD	5.1	1.9	2.3	1.5	1.1	1.0
10	20 000	Ave.	1039.4	998.9	993.2	22.1	19.4	19.0
		SD	2.3	1.1	1.0	0.6	0.4	0.4
25	8 000	Ave.	1013.8	999.3	998.6	12.4	11.8	11.7
		SD	1.0	0.9	0.9	0.4	0.3	0.3
50	4 000	Ave.	1006.9	1000.1	999.9	8.4	8.2	8.2
		SD	2.1	2.0	2.0	0.2	0.2	0.2
100	2 000	Ave.	1003.4	1000.2	1000.2	5.8	5.7	5.7
		SD	0.9	0.9	0.9	0.1	0.1	0.1
200	1 000	Ave.	1001.2	999.8	999.8	3.8	3.7	3.7
		SD	1.2	1.2	1.2	0.1	0.1	0.1
			(C) Right-skewed β-distribution					
2	100 000	Ave.	1224.6	1066.4	983.9	77.6	65.6	64.1
		SD	10.4	5.2	3.9	4.6	3.3	2.9
5	40 000	Ave.	1072.1	1005.1	988.7	31.6	28.1	27.5
		SD	3.0	1.2	1.1	0.8	0.6	0.6
10	20 000	Ave.	1032.8	1000.2	996.6	19.7	18.4	18.2
		SD	1.6	1.5	1.6	0.4	0.4	0.4
25	8 000	Ave.	1012.5	1000.0	999.5	11.5	11.2	11.2
		SD	1.2	0.9	0.9	0.2	0.2	0.2
50	4 000	Ave.	1006.3	1000.2	1000.1	7.9	7.8	7.8
		SD	1.1	1.0	1.0	0.2	0.1	0.1
100	2 000	Ave.	1003.0	1000.1	1000.1	5.4	5.4	5.4
		SD	1.3	1.3	1.3	0.1	0.1	0.1
200	1 000	Ave.	1001.5	1000.2	1000.2	3.5	3.5	3.5
		SD	1.4	1.4	1.4	0.1	0.1	0.1
			(D) Left-skewed β-distribution					
2	100 000	Ave.	1029.9	997.0	987.9	19.7	17.3	17.2
		SD	1.8	1.1	2.4	0.9	0.6	0.6
5	40 000	Ave.	1011.0	999.5	998.8	10.9	10.2	10.1
		SD	0.8	0.4	0.5	0.4	0.3	0.3
10	20 000	Ave.	1005.3	999.9	999.8	7.3	7.1	7.1
		SD	0.8	0.7	0.7	0.2	0.2	0.2
25	8 000	Ave.	1001.8	999.8	999.8	4.5	4.5	4.5
		SD	0.5	0.4	0.4	0.1	0.1	0.1
50	4 000	Ave.	1001.1	1000.1	1000.1	3.1	3.1	3.1
		SD	0.4	0.3	0.3	0.1	0.1	0.1

TABLE 2. (*Concluded*)

Sample size	No. of trials		Estimated population size			Root relative MSE[a]		
			$\hat{N}_1$	$\hat{N}_2$	$\hat{N}_3$	$\hat{N}_1$	$\hat{N}_2$	$\hat{N}_3$
100	2 000	Ave.	1000.7	1000.2	1000.2	2.1	2.1	2.1
		SD	0.4	0.4	0.4	0.1	0.1	0.1
200	1 000	Ave.	1000.3	1000.1	1000.1	1.4	1.4	1.4
		SD	0.4	0.4	0.4	0.0	0.0	0.0
		(E) Mixture of two normal distributions						
2	100 000	Ave.	1327.4	1223.7	1173.2	71.5	70.5	72.6
		SD	7.5	6.1	5.9	1.2	1.0	1.0
5	40 000	Ave.	1140.9	1053.4	1023.3	44.9	45.1	46.2
		SD	4.3	3.2	2.8	0.7	0.7	0.7
10	20 000	Ave.	1070.4	1012.9	1002.1	29.6	28.7	28.8
		SD	1.7	1.6	1.8	0.4	0.4	0.4
25	8 000	Ave.	1026.0	1001.0	999.1	17.0	16.5	16.5
		SD	2.8	2.4	2.3	0.3	0.3	0.3
50	4 000	Ave.	1013.2	1000.8	1000.4	11.6	11.4	11.4
		SD	3.0	2.9	2.9	0.2	0.2	0.2
100	2 000	Ave.	1005.5	999.6	999.5	7.8	7.7	7.7
		SD	2.4	2.4	2.4	0.2	0.2	0.2
200	1 000	Ave.	1002.2	999.5	999.5	5.2	5.1	5.1
		SD	2.3	2.2	2.2	0.1	0.1	0.1
		(F) Log-normal distribution						
2	100 000	Ave.	2525.8	2059.2	1790.9	335.8	285.3	266.8
		SD	118.0	93.6	80.9	26.3	21.8	19.8
5	40 000	Ave.	1557.2	1323.6	1212.2	124.1	106.7	102.6
		SD	48.1	39.3	35.1	8.3	7.2	6.8
10	20 000	Ave.	1278.9	1133.9	1077.6	70.8	63.6	63.2
		SD	24.2	18.8	16.6	4.6	4.1	4.1
25	8 000	Ave.	1113.8	1037.5	1018.3	38.3	36.5	36.8
		SD	11.4	9.5	9.3	2.3	2.1	2.2
50	4 000	Ave.	1054.5	1010.6	1003.7	25.1	24.6	24.8
		SD	8.8	6.6	5.8	1.9	1.9	2.0
100	2 000	Ave.	1028.8	1005.4	1003.5	17.0	16.9	16.9
		SD	6.1	5.0	4.7	1.3	1.4	1.5
200	1 000	Ave.	1011.9	1000.7	1000.3	11.1	11.1	11.1
		SD	4.3	3.4	3.3	0.9	1.0	1.0

[a]The square root of the relative mean square error, Root relative MSE = $\{\text{ave}[\sum(\hat{N}/N - 1)^2]\}^{1/2}$.

Ideally the estimates of N and the variance of the estimates would conform to normal distribution theory and the T values would follow the appropriate Student's t distribution. In many cases the distributions for T agreed closely with the distribution of Student's t (Fig. 4). However, with the extremely variable and skewed distributions (Fig. 4E and 4F) the T values were overdispersed relative to a Student's t statistic. The distributions of T often were skewed to the right, owing to right skewness in the distributions of $\hat{N}_2$ and positive correlation between $\hat{N}_2$ and $[\hat{V}(\hat{N}_2)]^{1/2}$.

Application to Real Fishery Data

To gain an appreciation for the bias that might arise from applying the standard estimator $\hat{N}_1$ to actual fishery data, I analyzed data collected in 1988 by port samplers from the Oregon Department of Fish and Wildlife (ODFW). The 30 samples were taken from landings at three Oregon ports of widow rockfish (*Sebastes entomelas*) that had been caught in bottom trawls. Because of time constraints the ODFW port samplers usually do not weigh each individual fish in a sample, but instead record the aggregate sample weight and the individual fish lengths.

I examined the length data to determine the major sources of variability. Box and whisker plots of the fish lengths (Fig. 5) illustrate the large variability both within and among samples. An analysis of variance of the length data indicated highly significant variation among samples, even when the samples were from the same port and quarter of the year (Table 4). If data on individual weights had been available, I presume they would have shown a similar pattern.

For my analysis of bias, I converted the individual fish lengths to weights using the following length–weight relationships;

$$\text{Males: Weight [g]} = 0.000\,010\,198\,(\text{length [mm]})^{3.066\,31}$$

$$\text{Females: Weight [g]} = 0.000\,002\,809\,0\,(\text{length [mm]})^{3.287\,81}$$

(ODFW, unpublished data). Then I applied the estimators $\hat{N}_1$ and $\hat{N}_2$ to the weight data.

The estimated fish weights varied considerably within samples, with the estimated coefficients of variation ($\hat{\sigma}_w/\hat{\mu}_w$)

Table 3. Monte Carlo evaluation of the estimated standard error of $\hat{N}_2$ (Equation (7)) and the distribution of T values. For the purpose of making comparisons, probability values for the theoretical Student's t-distribution are included at the bottom.

Sample size	No. of trials	SE	Distribution of T[a] $\lvert T\rvert \le 1$	$\lvert T\rvert \le 2$	$\lvert T\rvert \le 3$
		(A) Truncated normal distribution			
2	100 000	226.7	51.7	71.2	79.9
5	40 000	148.0	64.4	88.2	95.4
10	20 000	104.4	67.0	92.2	98.0
25	8 000	65.2	67.8	94.3	99.1
50	4 000	45.5	68.4	94.8	99.4
100	2 000	31.3	68.1	95.0	99.5
200	1 000	20.8	67.8	95.0	99.6
		(B) Uniform distribution			
2	100 000	633.7	55.4	71.1	78.1
5	40 000	316.5	68.5	87.7	93.8
10	20 000	204.4	70.8	91.3	96.9
25	8 000	120.8	69.5	93.9	98.5
50	4 000	82.8	69.0	94.6	99.1
100	2 000	56.5	68.0	94.9	99.4
200	1 000	37.5	68.5	95.2	99.6
		(C) Right-skewed β-distribution			
2	100 000	426.1	51.9	71.4	80.0
5	40 000	265.5	64.9	88.4	95.5
10	20 000	182.2	67.4	91.9	97.9
25	8 000	112.3	68.4	94.0	99.0
50	4 000	77.9	68.4	94.9	99.3
100	2 000	53.4	68.2	94.9	99.6
200	1 000	35.5	68.8	95.4	99.7
		(D) Left-skewed β-distribution			
2	100 000	149.2	51.3	68.5	76.6
5	40 000	100.7	65.0	86.5	93.6
10	20 000	71.1	67.2	91.1	97.1
25	8 000	44.5	67.7	93.6	98.7
50	4 000	31.1	68.1	94.5	99.3
100	2 000	21.4	68.3	95.3	99.6
200	1 000	14.2	68.8	95.3	99.7
		(E) Mixture of two normal distributions			
2	100 000	317.5	17.5	52.9	63.8
5	40 000	299.9	49.7	68.1	78.2
10	20 000	246.8	64.1	86.1	92.1
25	8 000	161.5	67.3	92.9	98.5
50	4 000	112.6	67.9	94.2	99.3
100	2 000	77.2	68.3	94.9	99.5
200	1 000	51.4	68.1	95.2	99.6
		(F) Log-normal distribution			
2	100 000	1131.5	48.1	68.5	78.3
5	40 000	638.9	53.1	81.8	92.6
10	20 000	446.4	55.2	85.1	95.5
25	8 000	294.3	58.7	88.5	97.5
50	4 000	214.7	61.5	90.9	98.6
100	2 000	153.8	63.5	92.5	99.1
200	1 000	105.4	65.3	93.8	99.3

Table 3. (*Concluded*)

Sample size	No. of trials	SE	Distribution of T[a] $\lvert T\rvert \le 1$	$\lvert T\rvert \le 2$	$\lvert T\rvert \le 3$
		Theoretical Student's t-distribution			
2			50.0	70.5	79.5
5			62.6	88.4	96.0
10			65.7	92.3	98.5
25			67.3	94.3	99.4
50			67.8	94.9	99.6
100			68.0	95.2	99.7
200			68.1	95.3	99.7

[a]$T = (\hat{N}_2 - N)/[(W/\bar{w})\overline{\mathrm{CV}}(\bar{w})]$, where $\overline{\mathrm{CV}}(\bar{w})$ was calculated using Equation (6).
[b]Degrees of freedom for the t-test are sample size − 1.

for individual samples ranging from 19 to 60%. However, because of the relatively large sizes of the individual samples (usually 30 fish per sample), the estimated coefficients of variation for the mean weights ($\hat{\sigma}_w/(\hat{\mu}_w\sqrt{n})$) were very small and there were trivial differences between the estimates $\hat{N}_1$ and $\hat{N}_2$ of the number of fish in the landings from which each sample was taken (Table 5). In this instance there was negligible bias in the estimates $\hat{N}_1$ for each sampled landing.

To derive estimates for the numbers of fish landed in each port–quarter combination, I had to consider the variability in mean fish weight among the different landings. I used weighted averages to combine the different sample average weights in each port–quarter combination, weighting each average by the estimated number of fish in that landing: $\mathrm{ave}[\bar{w}] = (\Sigma\hat{N}_i\bar{w}_i)/\Sigma\hat{N}_i$, where the subscript i is an index for the sample number and the summations are over the samples i = 1, 2, ..., m in each port–quarter combination. I calculated a standard error for each weighted mean using

$$\mathrm{SE}(\mathrm{ave}\bar{w}) = \left[(1 - m/M)\frac{\Sigma\hat{N}_i(\bar{w}_i - \mathrm{ave}[\bar{w}])^2}{\Sigma\hat{N}_i(m-1)}\right]^{1/2}$$

where M is the total number of landings in the port–quarter combination.

I then used the total weight of the landings by port and quarter and the estimated weighted averages and standard errors to calculate estimates $\hat{N}_1$ and $\hat{N}_2$ of the total number of fish in the port–quarter landings (Table 5). Because the average fish weights varied between samples and because there were small numbers of samples from each port–quarter combination, relative to the trivial differences between the estimates $\hat{N}_1$ and $\hat{N}_2$ for the sampled landings, there were much larger differences between the estimates $\hat{N}_1$ and $\hat{N}_2$ of the total numbers of fish landed from each port–quarter combination. However, the bias was still very modest; the largest relative difference was 3.3% (for Newport in the first quarter).

Discussion and Conclusions

The Monte Carlo tests confirm that the simple estimator $\hat{N}_1 = W/\bar{w}$, commonly applied in fisheries to estimate the total number of fish in a catch, can be highly positively biased and that the degree of bias depends on the sample size and the underlying variability in the fish weights. The results also indicate that the new estimators $\hat{N}_2$ and $\hat{N}_3$, which use sample information on the relative variability in average weight, are less biased than $\hat{N}_1$. However, these new estimators can remain substantially biased if sample

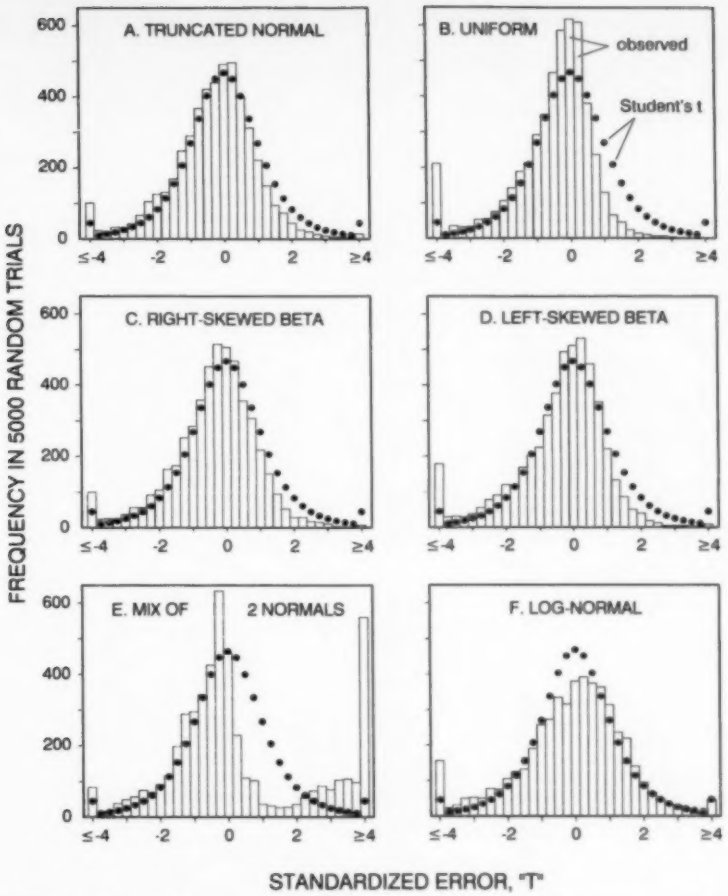

FIG. 4. Observed sample values of T (based here on 5000 trials with $n = 5$) were approximately distributed as Student's t.

TABLE 4. Analysis of variance for fish lengths observed in sampled landings from the Oregon fishery for widow rockfish during 1988.

Source	SS	df	MS	F^a
μ	25 179.6	915		
Trip	13 931.6	886	15.7	
Port	24 346.3	913		
Quarter	23 309.0	912		
Port + quarter	22 164.7	910		
Port × quarter	21 071.8	908		
Trip | μ	11 248.0	29	387.9	24.7**
Port | μ	833.3	2	416.7	26.5**
Quarter | μ	1 870.6	3	623.5	39.7**
Port + quarter | Port, μ	2 181.6	3	727.2	46.2**
Port + quarter | Quarter, μ	1 144.3	2	572.1	36.4**
Port × quarter | Port, quarter, μ	1 092.9	2	546.5	34.8**

[a]As the denominator for calculating the F statistics, I used the mean square error from the model with trip, in which each sample had its own mean length. This model provided the best fit to the observed length data. $^{**}P < 0.01$.

sizes are small or if individual fish weights are highly variable or skewed. There are two likely reasons for this result. The estimators $\hat{N}_2$ and $\hat{N}_3$ are based on the notion that the sample average weight is approximately normally distributed, but if sample sizes are small or if the weight distributions are highly skewed, this can be a poor approximation. Also,

TABLE 5. Estimates $\hat{N}_1$ and $\hat{N}_2$ for samples from the Oregon fishery for widow rockfish during 1988. Samples from three ports were used to estimate average fish weights for each port and quarter, which were then applied to the total landings for each port and quarter to estimate the total number of fish landed.

PORT (quarter)	Weight landed (kg)	Number fish sampled	Fish weight (g)		Estimated no. of fish landed	
			Mean	SE	$\hat{N}_1$	$\hat{N}_2$
ASTORIA (1)	5440	30	963.5	60.6	5 646	5 623
	13 205	30	702.8	35.8	18 789	18 741
	9 068	30	602.4	28.2	15 053	15 021
	12 846	30	681.1	27.0	18 860	18 831
	969	30	689.0	30.5	8 664	8 647
All trips	191 889	(209 landings)			276 373	275 249
Weighted mean weight using $\hat{N}_1$ =			694.3			
Weighted mean weight using $\hat{N}_2$ =			694.3			
ASTORIA (2)	3 007	29	1200.0	71.2	2 506	2 497
	2 099	30	865.6	50.3	2 425	2 416
All trips	67 860	(340 landings)			65 529	63 874
Weighted mean weight using $\hat{N}_1$ =			1035.6			
Weighted mean weight using $\hat{N}_2$ =			1035.6			
ASTORIA (3)	2 846	30	1245.1	64.7	2 286	2 279
	1 511	30	1146.4	77.6	1 318	1 312
	515	30	1093.9	66.4	471	469
	5 454	30	1176.1	63.4	4 637	4 624
All trips	132 177	(401 landings)			111 517	111 473
Weighted mean weight using $\hat{N}_1$ =			1185.3			
Weighted mean weight using $\hat{N}_2$ =			1185.3			
ASTORIA (4)	1 014	30	1206.9	74.2	840	837
	641	29	957.4	56.6	670	668
	1 094	30	1440.0	73.8	760	758
All trips	26 168	(203 landings)			21 604	21 343
Weighted mean weight using $\hat{N}_1$ =			1211.3			
Weighted mean weight using $\hat{N}_2$ =			1211.3			
COOS BAY (1)	1 471	30	950.3	52.5	1 547	1 543
	13 557	30	836.3	36.9	16 211	16 180
	3 628	30	1545.9	116.8	2 347	2 333
All trips	172 858	(348 landings)			186 290	180 948
Weighted mean weight using $\hat{N}_1$ =			927.9			
Weighted mean weight using $\hat{N}_2$ =			927.6			
COOS BAY (3)	12 571	30	1385.0	107.4	9 076	9 022
	434	31	1833.6	88.3	236	236
	6 883	30	1398.7	81.8	4 921	4 904
	8 278	30	836.6	38.0	9 894	9 874
	11 827	30	918.2	39.8	12 880	12 856
	13 435	30	921.4	32.8	14 581	14 562
	5 161	49	818.9	63.2	6 303	6 265
All trips	115 505	(218 landings)			114 131	113 229
Weighted mean weight using $\hat{N}_1$ =			1012.0			
Weighted mean weight using $\hat{N}_2$ =			1011.8			
NEWPORT (1)	1 194	30	913.0	41.2	1 308	1 305
	515	30	1411.9	101.7	365	363
	13 350	29	1523.7	54.2	8 761	8 750
	6 407	30	777.7	87.1	8 239	8 137
All trips	83 611	(179 landings)			72 732	70 447
Weighted mean weight using $\hat{N}_1$ =			1149.6			
Weighted mean weight using $\hat{N}_2$ =			1151.4			
NEWPORT (4)	1 286	30	1209.5	70.7	1 064	1 060
	1 037	29	1558.5	67.4	665	664
All trips	36 866	(120 landings)			27 434	27 009
Weighted mean weight using $\hat{N}_1$ =			1343.8			
Weighted mean weight using $\hat{N}_2$ =			1344.0			

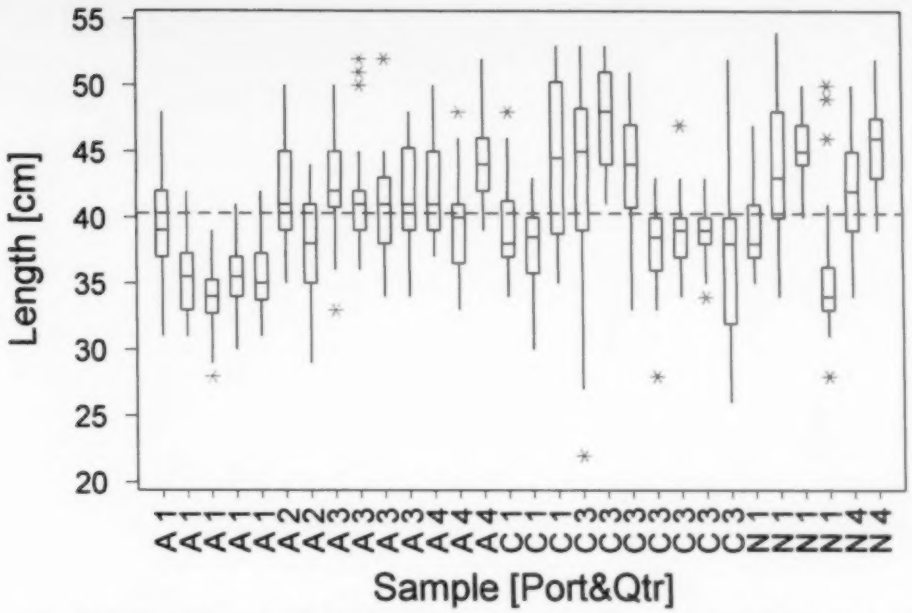

FIG. 5. Box and whiskers plot of the fish lengths observed in samples of widow rockfish (*Sebastes entomelas*) collected in Oregon during 1988. The codes "A," "C," or "N" on the horizontal axis indicate the port of origin (Astoria, Coos Bay, or Newport), and the numbers indicate the quarter of the year. The horizontal broken line represents the overall average length.

in deriving $\hat{N}_2$ and $\hat{N}_3$ the sample average and sample standard deviation were assumed to be independent random variables, which is not valid if sampling is done without replacement or is from a non-normal distribution.

The estimator $\hat{N}_1$ can be viewed as a special type of ratio estimator in which only the denominator of the ratio is a random variable. In general, ratio estimates based on random samples of n observations have bias of order $1/n$ (Cochran 1977); doubling the sample size will reduce the bias by half or better. For many fisheries the estimates $\hat{N}_1$ of the number of fish landed from a sampled landing will have negligible bias because reasonably large numbers of fish will have been sampled. However, the estimates of the total number of fish in all landings often will be based on a small number of sampled landings and can, therefore, be subject to much greater bias. The estimators $\hat{N}_2$ and $\hat{N}_3$ developed in this paper can be used to assess whether the bias may be important.

Modifying the sampling protocol provides an alternative solution to the problem of bias in the estimator $\hat{N}_1$. By taking samples with fixed weights of fish ($\sum w$) rather than fixed numbers of fish (n), the randomness in the ratio $(W/\sum w)n$ is moved from the denominator to the numerator, and in the limit as $E[n] \to \infty$ the number of fish in a sample is a random variable that follows an inverse Gaussian distribution with $E[n] = \sum w/\mu$ and $E[n](W/\sum w) = W/\mu$ (Johnson and Kotz 1970). With this type of sampling the standard estimator $\hat{N}_1 = W/\bar{w}$ is unbiased. This alternative methodology is not without problems, however. With a fixed-weight sampling scheme the usual estimator for average weight, $\bar{w} = \sum w/n$, is positively biased, $E[\bar{w}] = \sum w E[1/n] = \mu + \sigma^2/\sum w$. With either sampling scheme the problems of bias disappear rapidly as the sample size (or sample weight) increases.

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Diel Patterns of Drift by Five Species of Mayfly at Different Levels of Fish Predation

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Stream insects that drift downstream in the water column are at risk from fishes that feed visually in midwater, and the restriction of drifting to nighttime is hypothesized to have evolved as an avoidance response to this type of predator. I tested the hypothesis that low daytime drifting is a proximate response to the presence of drift-feeding fishes by manipulating fish density (brook trout, *Salvelinus fontinalis*) in two field experiments. Daytime drift activity of five prey taxa (all mayflies: Ephemeroptera) was low in both experiments and did not change following fish removal. By night, however, nighttime drift activity of two mayflies, *Baetis* and *Paraleptophlebia*, was increased in areas containing fish. The other three mayflies, *Ephemerella*, *Stenonema*, and *Eurylophella*, which showed less drift activity overall, displayed no consistent responses to fish presence. The original hypothesis predicts that risk from drift-feeding fishes should result in reduced daytime drifting. The increases in nighttime drifting away from patches dense with trout were not predicted by the original hypothesis, but may be an additional avoidance response to reduce long-term predation risk in streams where trout are distributed patchily in space.

Les insectes des cours d'eau qui dérivent en descendant le courant dans la colonne d'eau sont exposés aux poissons qui se nourrissent par repérage visuel dans les eaux intermédiaires et l'on suppose que le fait que les insectes ne dérivent que la nuit constitue une réaction d'évitement de ce type de prédateurs. Pour vérifier l'hypothèse voulant qu'une faible dérive diurne soit une réaction immédiate à la présence de poissons qui se nourrissent dans le courant, nous avons manipulé la densité du poisson (omble de fontaine, *Salvelinus fontinalis*) dans deux expériences sur le terrain. L'activité de dérive diurne de cinq taxons-proies (tous des éphéméroptères) était faible dans les deux expériences et n'a pas changé à la suite du retrait des poissons. La nuit, cependant, l'activité de dérive de deux éphéméroptères, *Baetis* et *Paraleptophlebia*, était accrue dans les zones poissonneuses. Les trois autres éphéméroptères, *Ephemerella*, *Stenonema* et *Eurylophella*, dont l'activité de dérive globale était moindre, n'ont montré aucune réaction constante à la présence du poisson. Selon l'hypothèse de départ, le risque lié aux poissons se nourrissant dans le courant aurait dû provoquer une diminution de la dérive diurne. Les augmentations de dérive nocturne hors des zones densément peuplées par l'omble de fontaine n'étaient pas prévues par l'hypothèse de départ, mais elles peuvent constituer une réaction d'évitement additionnelle visant à réduire le risque à long terme de la prédation dans les cours d'eau où l'omble est inégalement distribuée dans l'espace.

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Predators have important influences on behavioural decisions made by their prey, including decisions about when and where to engage in activities such as feeding, mating, and dispersal (Edmunds 1974; Sih 1987; Lima and Dill 1990). Prey often limit their activities to places and times which reduce their frequency of encounters with predators. Many taxa vulnerable to visual predators, for example, tend to enter areas containing these predators only at night because these predators usually feed ineffectively, or not at all, after dark. (e.g., Gentry 1974; Nelson and Vance 1979; Ohlhorst 1982; Edwards 1983; Holomuzki 1986; Haney 1988). Many benthic stream insects, including mayflies (Order Ephemeroptera), disperse by drifting short distances downstream in the water column (Waters 1972). Drifting insects are at risk from predatory fish that hunt by sight in midwater, and feed mostly during the day (Walsh et al. 1988; Angradi and Griffith 1990). Fish predation should select against behaviours that result in daytime drifting and, for this reason, the widespread pattern of concentrating drift activity in the hours of darkness (Waters 1972; Müller 1974) is hypothesized to have evolved as an avoidance response to drift-feeding fishes (Allan 1978).

Support for the predator-avoidance hypothesis comes from the observation that larger individuals of some insect species are more nocturnal than smaller ones (they show a greater ratio of night:day drift density) (Allan 1978, 1984; Skinner 1985). This supports the hypothesis because fish tend to select larger prey (e.g., Ringler 1979; Newman and Waters 1984); larger insects are therefore more at risk and so should be more nocturnal than smaller ones. More direct evidence for the hypothesis is that drift is less nocturnal in streams naturally lacking water-column predators than in streams where these predators are present (Malmqvist 1988; Flecker 1992; Douglas et al. 1994).

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Behaviours that evolved because they result in predator avoidance may be either fixed (sensu Stein 1979), where the prey no longer respond to present-day variation in predator density, or phenotypically plastic, in which case prey behaviour is varied according to the current risk. Diel behavioural shifts in other systems can be the result of either fixed or plastic responses to predators (e.g., Fawcett 1984; Neill 1992; Semlitsch and Reyer 1992). Early work on the drifting and activity patterns of stream invertebrates implicated light cues as regulators of nocturnal periodicity (Elliott 1965; Müller 1966; Holt and Waters 1967; Bishop 1969), suggesting that stream insects would not respond to present-day variation in the density of water-column predators (Allan 1978). More recent studies indicate, however, show that diel periodicity in feeding and positioning on the substratum can be the result of facultative responses to drift-feeding fishes (Culp and Scrimgeour 1993; Cowan and Peckarsky 1994). Further, several studies have demonstrated that stream insects alter their drift rates in response to predatory invertebrates (Corkum and Pointing 1979; Peckarsky 1980; Walton 1980; Malmqvist and Sjöström 1987) and benthic-feeding fish (Kohler and McPeek 1989; Culp et al. 1991); suggesting a potential for plastic drift responses to water-column predators.

Specific tests for flexibility of drift periodicity in response to the presence of drift-feeding fishes have produced varying results. Gammarid amphipods have shown both reduced (Williams and Moore 1985, 1989; Holomuzki and Hoyle 1990) and increased (Andersen et al. 1993) drift density and overall activity in the presence of midwater predators. Drift densities of insects have, however, usually been unaffected by manipulations of the density of drift-feeding fishes (Allan 1982; Williams 1990; Flecker 1992). Exceptions to this pattern are Williams' (1990) report that a few insect taxa increased their daytime drift density in response to trout removal, and Douglas et al.'s (1994) finding that a baetid mayfly reduced its daytime drift rate following trout addition. The varying results of these studies, and the lack of replication of the treatment in two of them (Allan 1982; Williams 1990), suggests a need for further tests for plastic responses of stream insects to drift-feeding fishes.

The aim of this study was to test whether drift periodicity is a fixed or plastic response to drift-feeding fishes by manipulating the density of drift-feeding fish in two field experiments and observing any resulting changes in the drift activity of five prey taxa. Specifically, the first experiment tested the combined effect of brook trout (*Salvelinus fontinalis*) and black-nosed dace (*Rhinichthys atratulus*) on drift densities of five mayflies, whereas the second experiment isolated the effect of brook trout on the propensity of mayflies to drift, measured as the rate of departure from a patch relative to benthic density within it. During both experiments, I also tested whether drift responses to fish were more strongly expressed in larger size classes of prey taxa, because larger insects are more vulnerable to drift-feeding fishes.

Methods

Study Site and Study Organisms

The experiments were done in Stoney Brook, New Hampshire, (43°23′N, 72°01′W), a second-order stream, 6 km long, which drains into Lake Sunapee, New Hampshire. The 0.6-km study section was located 3 km above the lake outlet (elevation = 300 m; mean summer discharge = 3.74 $m^3 \cdot min^{-1}$) and was shaded by riparian vegetation, consisting mostly of eastern hemlock (*Tsuga canadensis*) and mixed deciduous trees. Habitat in the experimental section was composed mostly of flowing riffles and runs, with a gravel and cobble substratum.

Fish populations were surveyed by electrofishing (pulsed direct-current, Smith-Root model 12) during August 1989, and June and August 1990 using the removal method (following Bohlin et al. 1989). Unblocked sections of stream (5–16 m long) were fished three times, 2–3 h apart, working upstream. The number of fish present ($\hat{y}$) was estimated as

$$\text{(1)} \quad \hat{y} = \frac{C_T}{1-(C_T - C_1/C_T - C_3)^3}$$

where C_T, C_1, and C_3 represent the total, first, and third catches respectively. Brook trout were present at densities ranging from 0.6 to 2.4·m^{-2} (mean = 1.2 ± 0.1·m^{-2} (SE)). The trout size distribution was bimodal, with one peak around 55–60 mm fork length (FL) representing young-of-the-year trout and a broader, shallower, peak around 80–110 mm FL representing older trout. During the day, brook trout feed predominantly on invertebrate prey drifting in midwater (McNicol et al. 1985; Grant and Noakes 1986; Forrester et al. 1994). The only other fish present were a few black-nosed dace (mean density = 0.009 ± 0.001·m^{-2}, which feed on benthic invertebrates (Johnson and Johnson 1982; Fuller and Hynes 1987).

The prey were five genera of mayflies (Ephemeroptera): *Baetis*, *Paraleptophlebia*, *Ephemerella*, *Eurylophella*, and *Stenonema*, the first two of which are bivoltine in Stoney Brook, whereas the last three are univoltine (G.E. Forrester, unpublished data). These mayflies constituted 29% of the benthic community in the study area and were all consumed by the brook trout (Forrester et al. 1994; Forrester 1994).

Experiment 1

The hypothesis that mayflies adjust their drift density according to the presence of fish was tested in a preliminary experiment in September 1989. Fish presence was manipulated in 35-m-long sections of stream, enclosed at the ends with mesh fences. Brook trout and black-nosed dace were present at natural densities in two stream sections, but were removed from two other sections. Drift densities of the five mayfly prey taxa were measured at the downstream end of each stream section 3 and 10 d after the fish manipulation.

Manipulation of fish density was done on 29–30 August by fencing the ends of the four contiguous sections of stream with hardware cloth (mesh size = 3 mm) that extended 10 cm into the sediment and 30 cm above the water's surface. Fish were removed from the sections second and furthest downstream by making four passes through each with an electrofisher. One pass was also made through the nonremoval sections to control for possible effects of electrofishing on drift rates.

Drift was sampled at the downstream end of each stream section on 2 and 9 September using a stationary drift net (mouth = 0.3 × 0.3 m square, net length = 1 m, mesh size = 0.3 mm). Drift was sampled from 13:00 to 23:00 on the first sampling date and the nets were emptied every 2 h. On the second date, however, sampling was done from 12:00 to 01:30 and the nets were emptied every hour, except between 18:00 and 20:30 when they were emptied every

half hour. To calculate the volume of water sampled by the nets, I measured the depth of water and current velocity at the net entrance before and after sampling (using a pygmy meter, Gurley Instruments). The drift samples were stored in refrigerated stream water after removing any large predatory invertebrates, and the mayflies were counted under a dissecting microscope within 4 d.

To ensure that all drift collected in a given section originated from within it, nylon mesh (mesh size = 0.15 mm) was placed over each of the fences 1 h before sampling started and then removed after sampling ceased. The mesh reduced flow in the upstream 1–2 m of the stream sections, but the drift measurements at the downstream end of the sections (33–34 m away) were unlikely to have been affected by the flow reduction. The mesh was cleaned with a brush halfway through the sampling interval to reduce clogging. Drift sampling was interrupted during cleaning, and for 15 min afterwards, to prevent capture of invertebrates disrupted by the cleaning process.

Mayfly drift densities were consistently low during the day, increased markedly after dark and remained at a fairly constant higher level throughout the night (Forrester 1992). I, therefore, pooled the samples into two groups, day and night, for statistical analyses. For 2 September, day samples were defined as those taken from 13:00 to 17:00 and night samples as those from 19:00 to 23:00. For 9–10 September, day samples were defined as those taken from 12:00 to 18:30 and night samples defined as those taken from 19:30 to 01:30. Drift samples straddling the dusk period were not used because their day–night status was uncertain. Differences in daytime and nighttime drift densities between fish removal and control sections were tested using repeated measures analyses of variance (ANOVA), with sample date as the repeated measure (Winer et al. 1991).

To test effects of fish on the size of drifting mayflies, I measured the head-capsule widths of the two most common mayflies, *Baetis* (n = 143) and *Paraleptophlebia* (n = 152). Measurements were made from a video display of a microscope image using a computerized image-analysis system. Measurements were pooled to calculate a mean size for each time of day (day and night), in each stream section, on each sampling date. These means were using as replicates in a repeated measures ANOVA to test effects of fish on the size of mayflies drifting during the day and at night. Sample sizes for *Paraleptophlebia* during the day were too small to permit analysis, so a test was performed only on the nighttime data.

Experiment 2

A second experiment was done in August 1990 to test the hypothesis that mayflies adjust their propensity to drift according to the density of brook trout. I manipulated trout density in fenced 35-m-long stream sections and removed all dace from the study area to isolate whether effects of fish in the first experiment were due to trout or dace. Trout densities in the stream sections were adjusted to one of three levels: (1) zero (no trout), (2) medium density (mean = 0.88 ± 0.02·m^{-2}, and (3) high density (mean = 1.56 ± 0.12·m^{-2}), with three replicate stream sections assigned to each treatment. Changes in drift of the five mayflies in response to trout manipulation were measured 6 and 10 d following the manipulation. Drift was quantified as the proportion of mayflies that drifted from small patches of substratum. This drift measure was adopted because it provides a better indication of mayfly behaviour than drift density, the measure used in the first experiment.

Experimental stream sections were enclosed at each end with a mesh fence made of hardware cloth (mesh size = 7 mm), and separated from one another by 17–20 m long unmanipulated areas. Trout-density treatments were established on 16–18 August by removing trout from zero-density sections with the electrofisher (four passes) and holding them in pens downstream. The remaining sections were also electrofished (three passes) to estimate trout densities, and to control for possible electrofishing effects on prey taxa. Trout numbers in high- and medium-density sections were then adjusted to the appropriate levels by adding trout from the holding pens, or removing trout, as necessary. Assignment of fish to sections was done so that different trout size-classes were roughly equally represented in each section.

Treatments were interspersed among sections in a way designed to reduce biases that might arise because a given stream section may receive trout cues and/or drifting mayflies from neighbouring upstream section(s). The assignment of treatments to stream sections, from upstream to downstream was as follows: high, high, zero, zero, medium, zero, high, medium, medium. Under this arrangement, the three sections immediately above the three zero-density sections were: a high-density, a medium-density, and a zero-density section. The same was true for the other two treatments, assuming that the unmanipulated area above the section furthest upstream was equivalent to a medium-density manipulated section. This should avoid any consistent bias that might have occurred if, for example, all of the zero-density sections were immediately downstream of high-density sections.

The propensity of mayflies to drift was measured from 2-m-long patches of gravel substratum with uniform flow (range of velocities = 21–29 cm·s^{-1}). A small fence (width = 1 m, mesh size = 1 mm) was placed across the upstream end of the patch to prevent sampling of mayflies drifting from upstream. The fence blocked drift of over 90% of mayflies (Forrester 1992), but reduced flow over the patch only slightly (mean reduction = 11%). Mayflies drifting from the patch were collected in a drift net placed across its downstream end for 2 h, starting 1 h after the fence was set up. A benthic sample (0.09 m^2) was then taken immediately upstream of the drift net. The drift propensity of mayflies was calculated as the number caught in the drift net divided by the number in the benthic sample. This calculation may be biased by variation in the area of substratum from which mayflies caught in the net originated, but any biases should be consistent among treatments so effects of trout can be tested.

Drift was measured in two randomly selected stream sections from each treatment on each of two dates (24 and 28 August). Two daytime (11:00–14:00) and two nighttime (19:30–21:30) measurements were made in each section on each date and the daytime and nighttime averages were used as replicates in analyses. Effects of trout density and sampling date on daytime and nighttime drift propensity were tested using ANOVA, where data from different dates were not considered repeated measures because they were taken in different stream sections.

To test for size-specific drift from the patches of substratum, I compared the head widths of mayflies that drifted

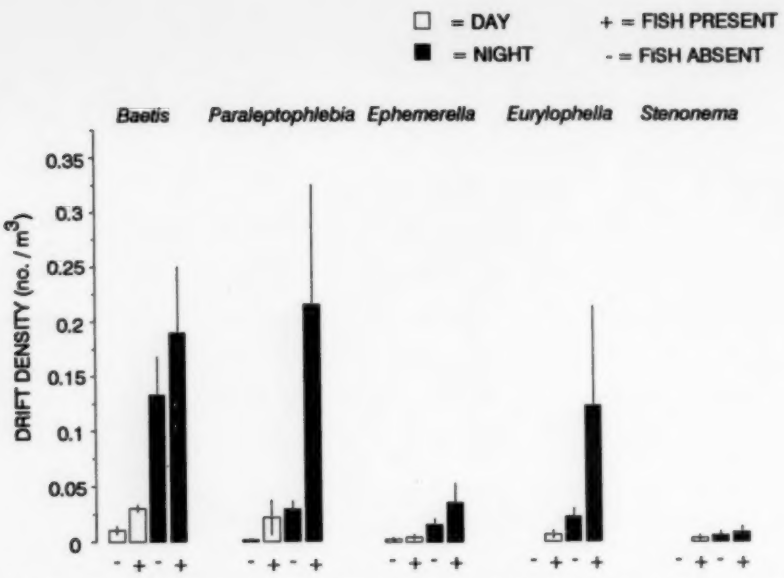

FIG. 1. Daytime and nighttime drift densities of five mayfly taxa in sections of stream where fish were either present at natural densities or had been removed (experiment 1). Error bars are standard errors.

during the night on 24 August with those that remained in the substratum (measurement technique described above). One pair of samples, consisting of mayflies that drifted from the patch (= drifting) versus those remaining in the sediment (= benthic), was picked from each of the stream sections. All of the mayflies in the chosen samples were measured, except some large benthic samples from which I measured only 10 individuals. In a few cases, mayflies from a second pair of samples were also measured to increase sample sizes. Measurements were pooled to generate a mean size for the benthic and drifting mayflies from each section and these section means were used as replicates in analyses. Effects of trout density and source (benthic vs. drifting) on the size of mayflies were tested using ANOVA.

As a second test for size-specific drifting, I compared the sizes of mayflies captured in drift nets placed at the downstream end of the sections with the size of mayflies collected in benthic samples randomly located within the sections. Drift was sampled for six, 1.5 to 2 h periods spaced over 24 h on 29 August by placing a drift net at the downstream end of each stream section. Two randomly located benthic samples (Surber samples; 0.09 m^2) were taken in each section after drift sampling ended. Samples were preserved in 70% alcohol and later sorted in the laboratory. Intact mayflies in the samples were measured (using the method described above). I pooled individual measurements to generate mean sizes of both benthic and drifting mayflies for each section. Effects of trout density and source (benthic versus drifting) on mayfly sizes were tested using ANOVA with section means as replicates.

Statistical Analyses

Most drift measurements involved subsampling within the replicate stream sections, but I always pooled subsamples and used stream sections as replicates when testing for effects of fish density to avoid inappropriately inflating the degrees of freedom for tests (see Hurlbert 1984). In addition to calculating the statistical significance of effects, I also calculated the proportion of the total variation in the data attributable to each term in the ANOVA models (following Vaughan and Corballis 1969; Dodd and Schulz 1973). Nonsignificant terms were removed from ANOVA models by pooling to allow more powerful tests for effects of fish density, but terms were pooled only if they explained less than 5% of the total variation in the data and if P was >0.25 (following Winer et al. 1991). When effects of fish density were not detected, I calculated the power of the test, i.e., my ability to detect an effect if, in fact, one existed. Power calculations were done following Cohen (1988) and Koele (1982), and are conditional on P (set at 0.05), the sample size, and the size of the effect to be detected. When I removed terms from ANOVA models by pooling, power calculations were made on pooled models because these were the ones used for significance testing.

The two experiments can be considered independent tests of the biological hypothesis that fish affect mayfly drift activity. P values from the two experiments can, therefore, be combined using Fisher's method to generate an overall P value for the hypothesis (Sokal and Rohlf 1981). I used this method when P values for effects of fish in both experiments were low ($P < 0.15$) but not conclusive individually, and the difference between means was in the same direction in both experiments.

Results

Effects of Fish on Drift Activity of Mayflies

Nighttime drift of *Baetis* was consistently increased by the presence of fish. During the first experiment, *Baetis* drifting at night were at higher densities in stream sections containing fish than in sections lacking fish ($F_{1,2} = 48.3$, $P = 0.02$) (Fig. 1). During the second experiment, nighttime

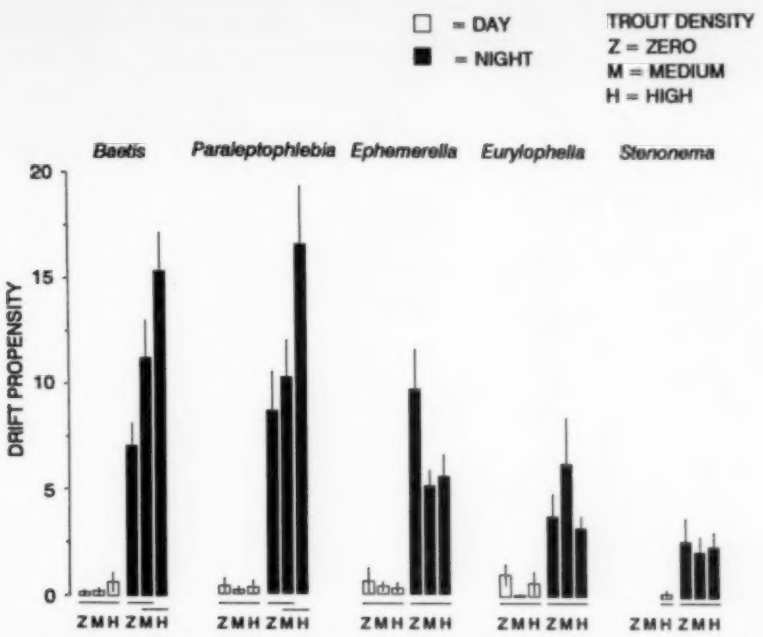

FIG. 2. Daytime and nighttime propensities to drift (drift rate divided by benthic density) from small (2-m-long) patches of substratum for five mayfly taxa exposed to different densities of trout (experiment 2). Error bars are standard errors. Horizontal lines underneath bars indicate means not significantly different at $P < 0.05$ (Tukey's HSD test).

drift propensity of *Baetis* increased with increasing trout density ($F_{2,8} = 17.3$, $P = 0.001$) (Fig. 2). The effect of trout in the second experiment was greater than that of fish in the first experiment, and explained 63% compared with 6.5% of variation in drift activity. Nighttime drift of *Paraleptophlebia* also increased at higher fish densities during both experiments (Fig. 1 and 2), but P values were too high individually to allow firm rejection of the null hypothesis (experiment 1: $F_{1,2} = 7.31$, $P = 0.11$; experiment 2: $F_{2,8} = 4.61$, $P = 0.046$). Combining the P values from the two experiments to calculate an overall P value for the effect of fish density on drift activity strengthens the conclusion that the presence of fish increases nighttime drift of *Paraleptophlebia* ($\chi^2 = 12.68$, df = 4, $P = 0.013$). The magnitude of response to fish was more consistent among experiments than for *Baetis*; fish density explained 31 and 47% of variation in drift of *Paraleptophlebia* during the first and second experiments, respectively.

Ephemerella showed a lower propensity to drift at night in stream sections containing trout than in sections without trout during the second experiment ($F_{2,8} = 7.81$, $P = 0.013$) (Fig. 2). Nighttime drift density was, in contrast, unaffected by fish in the first experiment ($F_{1,2} = 2.19$, $P = 0.28$), but the power of the test to detect an effect of the magnitude observed in the second experiment was low (power = 0.36). The weak test provided by the first experiment, and the fact that the difference between means was in the opposite direction in the two experiments (Fig. 1 and 2) precludes any firm conclusion about the effect of fish on *Ephemerella*.

I detected no influences of fish density on nighttime drift density or drift propensity of *Eurylophella* (experiment 1: $F_{1,2} = 0.85$, $P = 0.45$; experiment 2, analysis on log transformed data: $F_{2,8} = 2.70$, $P = 0.13$) and *Stenonema* (experiment 1: $F_{1,2} = 0.10$, $P = 0.79$; experiment 2: $F_{1,2} = 0.07$, $P = 0.94$) (Fig. 1 and 2). If *Eurylophella* had responded to trout to the same extent as *Baetis*, the response would probably have been revealed by the analyses (power = 0.44 and 0.83 for the first and second experiments respectively). For *Stenonema*, my chances of demonstrating a response of the strength exhibited by *Baetis* were slightly less (power = 0.44 and 0.66 for the first and second experiments, respectively) but, overall, I conclude that *Eurylophella* and *Stenonema* did not alter their drifts rates according to the local density of fish.

Daytime drifting by all five mayflies was low throughout (Fig. 1 and 2). *Baetis* tended to drift more frequently in the presence of fish in both experiments (Fig. 1 and 2), but the response was not significant in either experiment separately (experiment 1: $F_{1,2} = 9.62$, $P = 0.09$; experiment 2: $F_{2,8} = 0.93$, $P = 0.43$), nor when the two tests were combined ($\chi^2 = 6.50$, df = 4, $P > 0.1$). No significant responses to fish density were detected for any of the other four mayflies (P always >0.30) and the tests generally had reasonable power to detect effects of the magnitude shown by *Baetis* at night in the second experiment. For the first experiment power was 0.44 for *Baetis*, *Paraleptophlebia*, and *Eurylophella*, and the other two mayflies were too rare to test. For the second experiment power was 0.66 for *Eurylophella* and 0.83 for the other four mayflies. Overall, these results suggest that fish density does not influence the daytime drift activity of any of the five mayflies.

Effects of Fish on Size-Specific Drifting by Mayflies

Size distributions of *Baetis* were not influenced by the presence of fish in the first experiment (daytime: $F_{1,2} = 0.51$, $P = 0.51$; nighttime: $F_{1,2} = 1.34$, $P = 0.37$) (Fig. 3)

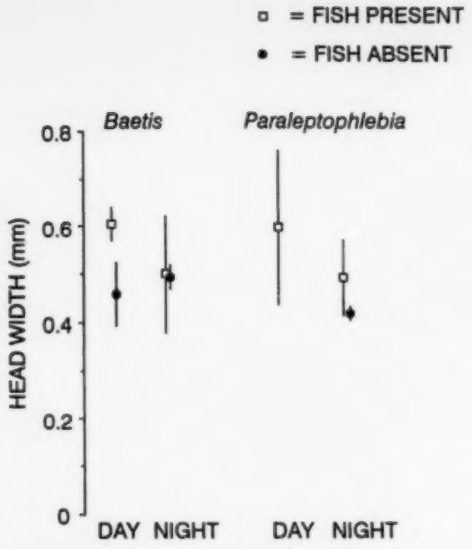

FIG. 3. Mean sizes of two mayfly taxa drifting in sections of stream containing or lacking fish (experiment 1). Error bars are standard errors.

nor by trout in the second experiment ($F_{2,5} < 1.49$, $P > 0.31$). *Baetis* that drifted in the second experiment were, however, significantly larger than those that remained in the substratum at all levels of trout density. This was true when mayflies were sampled from small (0.5 m^2) patches of substratum ($F_{1,5} = 12.5$, $P = 0.017$) (Fig. 4) and from 35-m stream sections ($F_{1,5} = 45.8$, $P = 0.001$) (Fig. 5), suggesting that larger *Baetis* were generally more prone to drift than smaller ones. Fish had no effect on the size distributions of *Stenonema* during the second experiment ($F_{2,5} < 0.79$, $P > 0.50$), but *Stenonema* drifting from small patches of substratum ($F_{1,5} = 7.20$, $P = 0.044$) and from entire stream sections ($F_{1,5} = 4.92$, $P = 0.077$) tended to be smaller than those that remained in the sediment at all levels of trout density. Drift of *Stenonema*, thus also appears to be size specific, but the pattern is in the opposite direction to that displayed by *Baetis*.

The average size of *Paraleptophlebia* drifting at night during the first experiment did not vary significantly according to the presence of fish ($F_{1,2} = 0.78$, $P = 0.47$) (Fig. 3). Trout density also had no influence on the size distribution of *Paraleptophlebia* during the second experiment ($F_{2,5} < 1.08$, $P > 0.40$), nor did drifting *Paraleptophlebia* differ in size from those that remained in the sediment ($F_{1,5} < 0.17$, $P > 0.69$) (Fig. 4 and 5). The mean sizes of the remaining mayflies, *Ephemerella* and *Eurylophella*, were similar in the drift and benthos ($F_{1,5} < 0.09$, $P > 0.78$) and were also uninfluenced by the density of trout ($F_{2,5} < 3.3$, $P > 0.12$) (Fig. 4 and 5).

Discussion

Daytime feeding by predatory fish in the water column should select against drifting during daylight hours. Surveys of streams naturally varying in predator presence (Malmqvist 1988; Flecker 1992; Douglas et al. 1994) and ontogenetic changes in drift periodicity (Allan 1978, 1984; Skinner 1985) provide good evidence that nocturnal drifting evolved because it results in the avoidance of drift-feeding fishes. If nocturnal drifting is a plastic response to fish presence, then drift should become less nocturnal (more evenly divided between day and night) following experimental fish removal. On the other hand, a lack of change in drift periodicity following predator manipulation supports the hypothesis that nocturnal drifting is a fixed avoidance behaviour.

Three of the five mayflies I studied did not alter their daytime or nighttime drift activity respond to the removal of drift-feeding fishes. Three prior studies in which drift-feeding fishes were removed also failed to detect subsequent changes in the drift periodicity of most taxa (Allan 1982; Williams 1990; Flecker 1992). The results of these experiments provide apparent support for the hypothesis that drifting has a fixed diel periodicity. Two other alternative explanations for the nondetection of plastic responses to drift-feeding fish cannot, however, be ruled out. The first is that responses to fish removal take longer to be expressed than the short duration (<2 wk) of these removal experiments (Magurran 1990; Semlitsch and Reyer 1992). The second possibility is that mayflies rely on chemical cues to assess fish presence. Water-borne chemicals may be transported large distances in streams so removal of fish from small areas of a stream might not remove these chemical cues. The experiments cannot, therefore, distinguish whether low daytime drifting is a fixed response or a plastic response to chemical cues released by fishes.

A solution to the confounding of removal experiments by chemical cues is to test for plastic responses by adding fish to areas of streams that otherwise lack fishes, or to work in laboratory streams filled with water never exposed to fish. In a recent study that adopted the former approach, trout addition cause reduced daytime drifting of *Baetis*, which suggests that the nocturnal peak in drift activity of this mayfly is a plastic avoidance response to trout (Douglas et al. 1994). Experiments using the second approach showed that the amphipod, *Gammarus pseudolimnaeus*, displayed reduced nighttime drift in laboratory streams when exposed to extracts from several fishes, including trout (Williams and Moore 1985, 1989). These results are also consistent with the predator avoidance hypothesis because prey may become more nocturnal in the presence of fish by either increasing daytime drift, reducing nighttime drift, or both.

Baetis and *Paraleptophlebia* both increased their rate of nighttime drifting at higher fish densities my experiments, a response that does not conform to the predator-avoidance hypothesis. The response to fish density during the first experiment could have been to either the brook trout or the black-nosed dace, or both. The rarity of dace, and the similarity to the results of the second experiment, when brook trout alone were present, suggests that effects on mayfly drift propensity were due primarily to brook trout. Another study recently reported a similar response to trout by the amphipod, *Gammarus pulex*, which displayed a transient increase in nighttime drifting but no change in daytime drifting after trout were stocked in two Danish streams (Andersen et al. 1993).

The behavioural mechanisms for, and adaptive significance (if any), of the nighttime responses to trout I observed is unclear. There are three potential mechanisms for increased drift by mayflies in the presence of brook trout: (1) the

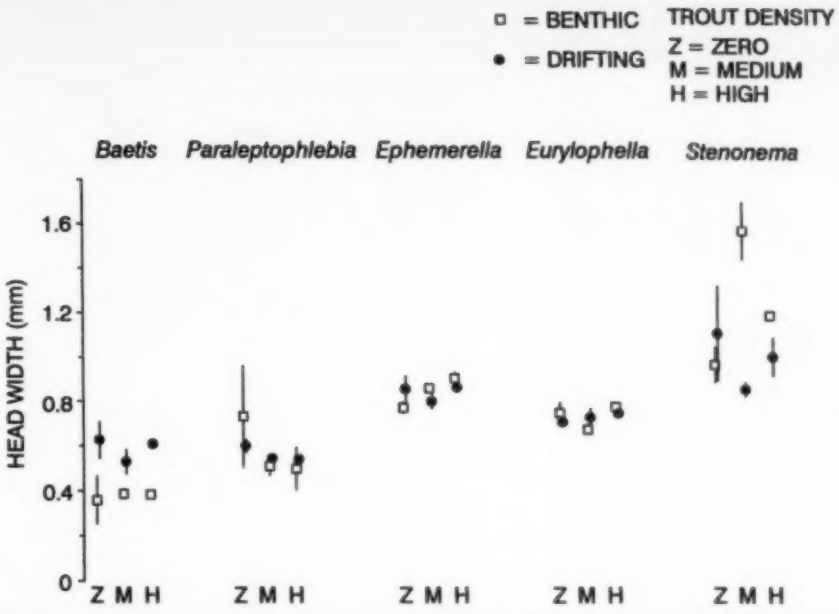

FIG. 4. Size-related patterns of drift for five mayfly taxa exposed to different densities of trout (experiment 2). Drifting mayflies are those departing from small (2-m-long) patches of substratum at night, benthic ones are those remaining in the sediment. Error bars are standard errors.

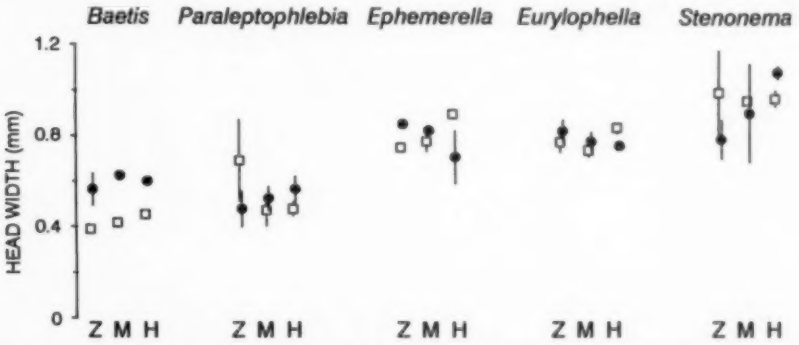

FIG. 5. Mean sizes of five mayfly taxa in 35-m-long stream sections stocked with different densities of trout (experiment 2). Open squares indicate mayflies from benthic samples within the section and solid circles indicate mayflies collected in drift nets at the downstream ends of the sections. Other symbols as for Fig. 4. Error bars are standard errors.

mayflies altered other behaviours, such as positioning on the substratum or locomotor activity, which increased their probability of being dislodged into the water column; (2) the mayflies increased their rate of entry into the water column or distance drifted directly; or (3) mayfly behaviour was unchanged and trout were physically dislodging them from the substratum.

Physical dislodgments as a result of benthic foraging by trout cannot be excluded as a possibility because, although stomach content analyses indicate that salmonids feed mostly by day, a low level of nighttime feeding does occur (Allan 1981; Walsh et al. 1988; Sagar and Glova 1988; Forrester et al. 1994; for an exception see Elliott 1973). Indirect evidence indicates that brown (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are capable of feeding on drifting prey at night (Jenkins 1969), but there no direct observations of nocturnal foraging by trout, so whether they feed only in midwater or switch to some degree of benthic foraging is unknown.

Baetis and *Paraleptophlebia* show increased drifting in the presence of benthic fish (Kohler and McPeek 1989; Culp et al. 1991) and predatory invertebrates (Corkum and Pointing 1979; Peckarsky 1980; Malmqvist and Sjöström 1987). Drifting in these studies was not correlated with changes in positioning or activity, suggesting that drifting was not a byproduct of these other behaviours. *Baetis* (Charnov et al. 1976; Culp and Scrimgeour 1993; Cowan and Peckarsky 1994) and other stream invertebrates (Williams and Moore 1985, 1989; Andersson et al. 1986; Feltmate et al. 1986; Feltmate and Williams 1989; Holomuzki and Hoyle 1990) do,

however, show altered positioning and activity in the presence of drift-feeding fish, so changes in these other behaviours could also potentially account for increased nighttime drifting by *Baetis* and *Paraleptophlebia* in my experiment.

Predator-avoidance behaviours are often size specific when the risk of predation varies among prey size-classes (Bertness et al. 1981; Sih 1982; Harvey 1991; Culp and Scrimgeour 1993). None of the mayflies, however, showed size-specific drift responses to brook trout density. There was also no tendency for the larger mayfly taxa to be the ones that responded to trout. This result was perhaps not surprising, because the mayfly responses to trout all occurred at night. Selection by trout for larger prey is strong during the day, but is weak or nonexistent at night (Allan 1978; Forrester et al. 1994) and so nighttime responses would not be expected to be size specific.

Increased behavioural drifting at night by *Baetis* and *Paraleptophlebia* exposed to high trout densities would imply that the benefits of this behaviour outweigh the immediate risk of being consumed by trout while drifting. Increased drifting might be an effective response to encounters with trout if a high proportion of nighttime feeding is on the benthos. If, instead most nighttime feeding by trout is in the water column then this behaviour appears, at first sight, to be maladaptive. One potential explanation for such a response, however, arises from the fact that trout are often patchily distributed in space over tens of metres (e.g., Egglishaw and Shackley 1977; Bohlin 1978; Bowlby and Roff 1986; Newman and Waters 1989). *Baetis* and *Paraleptophlebia* nymphs therefore pass through many patches of varying trout density in their several months of nymphal life. Under these circumstances, drifting more frequently at night from patches of high trout density would result in spending a greater proportion of the daytime in patches of low predator density, when summed over several months. Because risk from trout is greater during the day than at night, this strategy may reduce the long-term risk of predation by trout.

Most studies of how prey respond to risk from visual predators have focused on activities that take place during the day (Stein 1979; Sih 1987; Lima and Dill 1990). The results of my experiments, and those of Andersen et al. (1993), suggest that visual predators can also influence the nighttime behaviour of some taxa. These influences are not well understood and there is a need for further studies of the interactions between visual predators and their prey that occur after dark.

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Seasonal Consumption by Dace (*Phoxinus eos* × *P. neogaeus*): A Comparison between Field and Bioenergetic Model Estimates

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We compared the predictions of two bioenergetic models with independent field-derived estimates of consumption rates for dace (*Phoxinus eos* × *P. neogaeus*). These two models differ only in the energy that fish allocate to standard metabolism and activity. Daily ration and body mass of age 3$^+$ dace from Lake Triton were estimated on 29 occasions during a 67-d period (June 22 – August 27, 1992). Water temperature and caloric density of fish and food were also monitored. Fish growth was on average 2.5 cal·d^{-1} (1 cal = 4.19J). Observed cumulative consumption for an average fish was 7.6 kcal. Seasonal consumption predicted by the first and second models was 33.5 and 6.5 kcal, respectively. The prediction of the second model was not significantly different from our direct estimate. The second bioenergetic model can be used to accurately predict the feeding rate of dace in the field by using models of maximum standard respiration (MSR) currently available in the literature (intercept = 0.015, slope = −0.2) with an activity multiplier of 1. Alternatively, because these models often include energy expenditures associated with digestion and/or activity, a MSR model having an intercept of 0.006 with an activity multiplier of 3 can also be used.

Nous avons comparé les prédictions de deux modèles bioénergétiques du ventre rouge (*Phoxinus eos* × *P. neogaeus*) avec une estimation indépendante in situ de la consommation. Ces deux modèles ne diffèrent qu'au niveau de l'énergie alloué par le poisson au métabolisme standard et à l'activité. La ration journalière et la masse des ventres rouges (3$^+$) du lac Triton ont été estimées à 29 reprises sur une période de 67 jours (22 juin au 27 août 1992). La température de l'eau, la densité calorique des poissons et des proies ont également été suivies. La croissance des poissons a été en moyenne de 2,5 cal·d^{-1} (1 cal = 4.19J). La consommation cumulative observée in situ pour un poisson moyen était 7,6 kcal. Les taux de consommation prédits par le premier et le deuxième modèles étaient 33,5 et 6,5 kcal, respectivement. La prédiction du second modèle n'était pas significativement différente de notre estimation directe. Le deuxième modèle bioénergétique peut être utilisée pour prédire adéquatement les taux de consommation du ventre rouge en utilisant les modèles de respiration standard maximale (RSM) actuellement disponible dans la littérature (ordonnée à l'origine = 0,015; pente = −0,2) et d'un coefficient d'activité de 1. Puisque ces modèles incluent souvent des dépenses énergétiques associées à la digestion et/ou à l'activité, un modèle de RSM ayant une ordonnée à l'origine de 0,006 avec un coefficient d'activité de 3 peut être également utilisé.

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Bioenergetic models provide useful insights on growth processes (Rice et al. 1983), predator–prey dynamics (Stewart et al. 1981), nutrient recycling (Kraft 1992), bioaccumulation of pollutants (Borgmann and Whittle 1992), and fish-management strategies (Stewart et al. 1981; Bevelheimer et al. 1985; Ruggerone and Rogers 1992). These models partition consumption into growth, respiration, and waste (Kitchell et al. 1977). Equations that describe fish physiological processes are generally derived from laboratory studies and assume that they adequately represent the field situation. Furthermore, parameter values used to construct bioenergetic models of poorly studied fish species are often borrowed from well-studied species (Ney 1990, 1993).

Bioenergetic models have been evaluated for several fish species (mostly piscivorous fishes) by comparing predicted fish growth or consumption rates to field-derived values. However, the adequacy of bioenergetic model predictions remains the subject of a debate (Boisclair and Leggett 1991; Hewett et al. 1991). Evaluation of these models has produced contradictory results, including good fits (Rice and Cochran 1984; Olson and Boggs 1986; Beauchamp et al. 1989; Brodeur et al. 1992; Kraft 1992; Ruggerone and Rogers 1992; Hewett and Kraft 1993) and poor fits (Minton and McLean 1982; Diana 1983; Boisclair and Leggett 1989; Post 1990; Fox 1991; Wahl and Stein 1991; Madon and Culver 1993). Evaluation of bioenergetic models requires the estimation of fish weight and growth, water temperature, fish and prey caloric density, and the indigestible fraction of the prey in the diet (Hewett and Johnson 1987, 1992). Accurate independent estimates of feeding rates are also required (Diana 1983; Ney 1990, 1993).

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Field-derived consumption rates are usually obtained by integrating time series of daily rations obtained at 2-wk to 2-mo intervals. This procedure assumes that the quantity of food consumed by fish does not vary substantially over consecutive days. It has been suggested that this assumption can introduce large errors in seasonal or yearly consumption estimates (Smagula and Adelman 1982). This may be particularly true for piscivores that eat large prey (Smagula and Adelman 1982; Diana 1983; but see Trudel and Boisclair 1993 for planktivorous species). Interestingly, most field evaluations of bioenergetic models (8 of 14) were performed on piscivorous fish. Furthermore, several studies (12 of 14) designed to evaluate bioenergetic models did not account for the seasonal variation in fish and prey caloric density. Stewart and Binkowski (1986) showed that seasonal consumption rates estimated from bioenergetic models could be biased by as much as 50–100% when seasonal changes in fish and prey caloric density were not considered. Consequently, additional evaluations of the bioenergetic models are required before their predictions can be accepted with confidence (Ney 1990, 1993; Wahl and Stein 1991; Hansen et al. 1993).

The objective of this study was to evaluate the bioenergetic model of a hybrid dace (*Phoxinus eos* × *P. neogaeus*; Legendre 1970). Bioenergetic models can be used to predict growth from consumption estimates, or to predict consumption from growth data. In this study, we used the bioenergetic model to predict food consumption of dace using growth data. This strategy was adopted because bioenergetic models are expected to be most efficient at predicting consumption rates (Kitchell et al. 1977; Stewart et al. 1983; Bartell et al. 1986; Hewett and Johnson 1987, 1992). We, therefore, evaluated the bioenergetic model of dace by comparing consumption rates predicted by the model to field-derived values. In contrast with most evaluations of bioenergetic models, we estimated daily ration at a high sampling frequency (29 daily ration estimates over a 67-d period) and also estimated the seasonal variation of fish and food caloric density.

Methods

Evaluation of the bioenergetic model of fish requires the estimation of fish growth and consumption rates using a common energy unit (calories or joules). Estimation of fish growth requires data on the variation of fish weight over time and the determination of their caloric density. Estimation of the quantity of food consumed by fish during 1 d requires data on the diel variation of their digestive tract contents, the determination of their evacuation rate during that day, and the determination of food caloric density (Eggers 1977; Elliott and Persson 1978; Jobling 1981; Olson and Mullen 1986). The variation of fish weight and of their digestive tract contents, and their evacuation rates were determined in the field, while the caloric density of fish and their prey were determined in the laboratory.

Species and Study Site

The study was performed using a natural population of hybrids of redbelly dace and finescale dace (*Phoxinus eos* × *P. neogaeus*). Sampling was conducted in Lake Triton (45°59′N, 74°00′W), a small (area = 1.8 ha; maximum depth = 3.6 m) mesotrophic lake (total phosphorus = 8.1 $\mu g \cdot L^{-1}$; S. Masson, Département de sciences biologiques, Université de Montréal, personal communication) located at la Station de Biologie des Laurentides de l'Université de Montréal (70 km northwest of Montreal), in the lower Laurentian region of Quebec. This lake was selected as a study site because its high dace biomass and density (Magnin et al. 1976; Trudel and Boisclair 1993) could sustain the intense sampling required by our work.

Field Procedure

Fish were sampled on 29 occasions from June 22 to August 27, 1992, to estimate growth and consumption rates. On each sampling date we collected 40 dace ranging from 40 to 70 mm (total length). Scale examination (Frost 1943) indicated that dace of this size were age 3^+ fish. Ten fish were collected at 6-h intervals over a period of 24 h beginning at 07:00. This sampling interval has repeatedly been shown to be adequate to estimate the daily ration of planktivorous and benthivorous fish species (Boisclair and Leggett 1988; Boisclair and Marchand 1993). Fish were captured using one to three unbaited minnow traps (80 × 32 cm; 0.36-cm^2/mesh) during daytime and using a knotless nylon seine (20 × 2 m; 0.2-cm mesh) at night. Minnow traps were never set for more than 15 minutes. The locations of the traps were randomized within the lake. In a previous study (Trudel and Boisclair 1993), we have shown that mean quantity of food found in the complete digestive tract of dace captured in traps was not significantly different from that of dace sampled simultaneously by seining (mean difference was less than 9%).

Dace were killed by an overdose of 2-phenoxyethanol (1 $ml \cdot L^{-1}$) immediately following capture. Ten fish were selected randomly from each sample and retained to estimate consumption rates. Total blotted weight was noted (±0.01 g). Total digestive tract contents (no well defined stomach is present in this species) were removed within 1 h of capture, dried (60°C for 24 h), and weighed using an electronic balance (±0.0001 g).

Laboratory Procedure

Fish growth and consumption rates were defined using caloric densities. The caloric density of five dace ($cal \cdot g^{-1}$ dry wt.) was determined on June 1, July 15, and August 25, 1992, using a microbomb calorimeter (Philipson 1964). The caloric density of the food consumed by dace was determined using fish diet and prey caloric-density values from Cummins and Wuycheck (1971). The diet of dace was described by sampling 10 fish during the peak of the feeding cycle on June 29, July 9 and 26, August 2 and 26, 1992. The complete digestive tract content of each fish was removed and placed in a Ward cell to facilitate counting and identification of prey. Zooplankton were an important prey of dace in Lake Triton, particularly in August (see Results). Schindler et al. (1971) and Snow (1972) reported that the variation of zooplankton caloric density during the summer was, on average, less than ±10% of the mean value. Consequently, seasonal variation of the caloric value of diet was represented by the variation of its taxonomic composition.

Computations and Analyses

Growth

Absolute growth rate (G; $cal \cdot d^{-1}$; 1 cal = 4.19J) was estimated by regressing mean caloric contents of dace with the

day of the year. The slope given by the regression analysis was taken as the absolute growth rate. Mean caloric contents of dace on a given day were estimated by multiplying their mean weight (geometric mean) with their average caloric density, assuming that the dry weight represented 22% of the wet weight (M. Trudel and D. Boisclair, unpublished data). Average fish caloric densities were 1329, 1270, and 1357 cal·g^{-1} wet wt. on June 1, July 15, and August 25, 1992, respectively. Fish caloric density did not vary significantly among sampling dates ($F_{2,12} = 1.27$; $p > 0.3$). Therefore, we used a value of 1320 cal·g^{-1} wet wt. for fish caloric density for our modeling purposes.

Diet

The relative contribution of each prey type (P_i; percent) to the diet of a fish was expressed as a percentage of the total number of prey consumed by that fish. The caloric density of food (CDF) was then estimated as

$$(1) \quad \mathrm{CDF} = \sum_{i=1}^{n} \mathrm{CDP}_i \cdot P_i$$

where CDP_i is the caloric density of prey i and n is the number of taxa consumed by dace. Linear interpolation was used to estimate food caloric density between sampling dates.

Digestive tract contents

The dry weight of the digestive tract contents relative to the wet weight of the fish (F_i; g·100 g^{-1}; further referred to as gut fullness) was estimated for each dissected fish as

$$(2) \quad F_i = \left(\frac{G_i}{W_i}\right)100$$

where G_i (g) is the dry weight of the digestive tract contents of fish i, and W_i (g) is the wet weight of that fish. Mean gut fullness was estimated using the arcsin($\sqrt{F_i/100}$) transformation for each sampling date to eliminate heteroscedasticity and to normalize gut fullness indices (Sokal and Rohlf 1981; Boisclair and Leggett 1988; Trudel and Boisclair 1993).

Evacuation rate

Evacuation rate (R; h^{-1}) of dace was defined as the maximum rate at which food was evacuated from the complete digestive tract during a specific time interval of the feeding cycle (Boisclair and Leggett 1985; Boisclair and Marchand 1993). This approach assumes that fish were not feeding during this interval. Evacuation rate of the digestive tract contents of dace was assumed to be adequately represented by an exponential decay model. Therefore, R was estimated using the geometric mean gut fullness of fish at the beginning (F_t) and at the end (F_{t+6}) of each 6-h interval as

$$(3) \quad R = \frac{\ln F_{t+6} - \ln F_t}{6}$$

To maximize the probability of satisfying the assumption that fish were not feeding during a given 6-h interval, we estimated R only when there was a significant and sharp decrease in the mean digestive tract content at the beginning and at the end of the interval. We used the highest value of R estimated from all the feeding cycles to estimate food consumption rate on every sampling date.

Standard error of R was estimated using the bootstrap method (Efron 1985). For each sampling interval that was used to estimate R, 10 fish were sampled with replacement at time t and $t + 6$ to estimate the initial and final mean gut fullness. A bootstrap estimate of R was then calculated using Equation (3). This procedure was repeated independently 1000 times. The standard deviation of the 1000 bootstrap estimates of evacuation rate was taken as the true standard error of R (Efron 1985).

Estimation of consumption rates

Mean daily ration (C_d; g dry wt.·100 g^{-1} wet wt.·d^{-1}) was calculated using the Eggers (1977) model as modified by Boisclair and Leggett (1988):

$$(4) \quad C_d = F_d \cdot R \cdot 24$$

where F_d is the mean gut fullness (back transformed from arcsin($\sqrt{F_i/100}$); g dry wt.·100 g^{-1} wet wt.) on day d, R is the evacuation rate (h^{-1}) and 24 is the number of hours in a day.

Estimation of the error associated with daily ration values requires simulations that account for the error around F_d and evacuation rate R (Boisclair and Leggett 1988; Trudel and Boisclair 1993). We used Monte Carlo simulations to account simultaneously for the error associated with F_d and R. The pseudovalue of daily consumption rate (C_i; g dry wt.·100 g^{-1} wet wt.·d^{-1}) was estimated as

$$(5) \quad C_i = F_i \cdot R^* \cdot 24$$

where F_i is the gut fullness of fish i, and R^* is a pseudovalue of evacuation rate. This operation was performed using every fish (n = 40 fish·d^{-1}). R* was calculated as

$$(6) \quad R^* = R + (\mathrm{SE}_R \cdot \mathrm{RN})$$

where R is the evacuation rate, SE_R is the standard error of R, and RN is a normally distributed random number having a mean of 0 and a standard deviation of 1. A different RN was generated each time an R^* value was calculated.

Cumulative consumption by dace over the complete duration of our study (67 d) and its 95% confidence interval (CI) was estimated using Monte Carlo simulations. A pseudovalue of daily ration (C_d^*) were generated independently on each sampling day as

$$(7) \quad C_d^* = C_d + (\mathrm{SE}_C \cdot \mathrm{RN})$$

where C_d is the mean daily ration on sampling day d, SE_C is the standard error of the mean daily ration. Linear interpolation was used to estimate pseudovalues of daily ration between sampling dates. Pseudovalues of daily ration were transformed into calories using food caloric density. Cumulative consumption was estimated as the sum of pseudovalues of daily ration over the 67-d period. This procedure was repeated 1000 times. The mean and the 95% CI of cumulative consumption on any given day were defined respectively by the 50th percentile and by the 2.5th and 97.5th percentile of the 1000 pseudovalues of cumulative consumption determined for that day.

Bioenergetic model

The bioenergetic model we used to predict the food consumption of dace was based on physiological studies performed by McCormick (1976), Wootton et al. (1980), and Cui and Wootton (1989). The general equation of the bioenergetic model can be written as

$$(8) \quad C = G + \mathrm{SMR} + \mathrm{HI} + F + U + A$$

where C is the quantity of food consumed, G is the growth (somatic + gonadal), SMR is the standard metabolic rate,

TABLE 1. Parameter values for the PS1 and PS2 bioenergetic models of dace (Hewett and Johnson 1987, 1992).

Symbol	Parameter description	PS1	PS2
	Consumption		
CA	Intercept for maximum consumption	0.36	0.36
CB	Slope for maximum consumption	−0.31	−0.31
CTO	Optimum temperature for consumption	26	26
CTM	Maximum temperature for consumption	29	29
CQ	Slope for temperature dependence of consumption	2.3	2.3
	Respiration		
RA	Intercept for maximum standard respiration	0.04	0.0148
RB	Slope for maximum standard respiration	−0.20	−0.20
RTO	Optimum temperature for standard respiration	29	29
RTM	Maximum temperature for standard respiration	32	32
RQ	Slope for temperature dependence of standard respiration	2.1	2.1
ACT	Active respiration multiplier	2.0	1.0
S	Heat increment	0.15	0.15
	Waste losses		
FA	Fecal losses coefficient	0.40	0.40
UA	Urinary losses coefficient	0.10	0.10

HI is the heat increment or the cost associated with digestion (Beamish and Trippel 1990), F and U are fecal and urinary losses, respectively, and A is the energy allocated to activity. Each physiological component was defined as a rate expressed in $cal \cdot d^{-1}$. Standard metabolism is a function of fish weight and water temperature. Heat increment, fecal losses, and urinary losses are defined as constant fractions of the quantity of food consumed, while activity is assumed to be a fixed multiple of standard metabolic rate.

Two sets of parameters were used to estimate each component of Equation (8). The parameters presented by Hewett and Johnson (1987, 1992), further referred to as parameter sets 1 (PS1) and 2 (PS2), differ only in the energy allocated to standard and active metabolism (Table 1). PS1 allocates more energy to standard and active metabolic rates than PS2. The two versions of the model were implemented on a daily basis. Linear interpolation was used to estimate values of fish weight, fish and food caloric density, and water temperature between sampling dates.

Monte Carlo simulations were used to evaluate the influence of the error around initial fish weight, and growth rate on food consumption estimates obtained using the Hewett and Johnson (1987, 1992) models. Pseudovalues of initial fish weight (M^*) and growth rate (G^*) were generated independently as

$$M^* = M + (SE_M \cdot RN) \quad (9)$$

$$G^* = G + (SE_G \cdot RN) \quad (10)$$

where M is the mean initial weight of dace, SE_M is the standard error of mean fish weight, G is the growth rate of dace, and SE_G is the standard error of the mean growth rate. The bioenergetic model was then implemented with one pseudovalue of initial weight and growth rate to estimate the cumulative consumption of dace for each simulation. We produced 1000 independent estimates of cumulative consumption curves for PS1 and PS2. The mean and the 95% CI of cumulative consumption on any given day were defined, respectively, by the 50th percentile and by the 2.5th and 97.5th percentiles of the 1000 pseudovalues of cumulative consumption determined for that day.

Results

Fish Weight and Growth

Mean fish weight (back transformed from natural logarithm) ranged from 1.15 (July 10) to 1.58 g wet wt. (August 4) and varied significantly among sampling dates ($F_{28,1131} = 2.13$; $p < 0.001$) (Fig. 1). Initial and final weight were 1.30 and 1.35 g wet wt., respectively. The 95% CI around fish weight was on average ±9.0% of the mean value. Fish weight tended to increase by 0.0019 g wet $wt \cdot d^{-1}$ during the study ($F_{1,27} = 4.71$; $p < 0.05$; $r^2 = 0.16$). Absolute growth rate of dace was 2.5 $cal \cdot d^{-1}$ ($SE_G = 1.2$ $cal \cdot d^{-1}$). Predicted final weight of dace using their initial weight and their growth rate was 1.43 g wet wt., and differed only by 5.9% from the observed final weight.

Diet and Prey Caloric Density

The diet of dace was essentially composed of zooplankton (cladocerans and copepods) and aquatic insects (Odonata and Ephemeptora) throughout the summer (Table 2). Aquatic insects were the major prey in the diet of dace in July and represented more than 80% of the encountered prey (Table 2). The diet of dace gradually shifted to zooplankton in August, and zooplankton represented more than 80% of the consumed prey at the end of this month (Table 2). Food caloric density estimated using fish diet and prey caloric density values from Cummins and Wuycheck (1971) ranged from 5298 (July 9) to 5322 $cal \cdot g^{-1}$ dry wt. (August 26).

Evacuation Rates

Evacuation rates (R), determined from all the feeding cycles analyzed, ranged from 0.21 to 0.24 $\cdot h^{-1}$ (Table 3). The 95% CI of R was, on average, ±36.7% of the mean

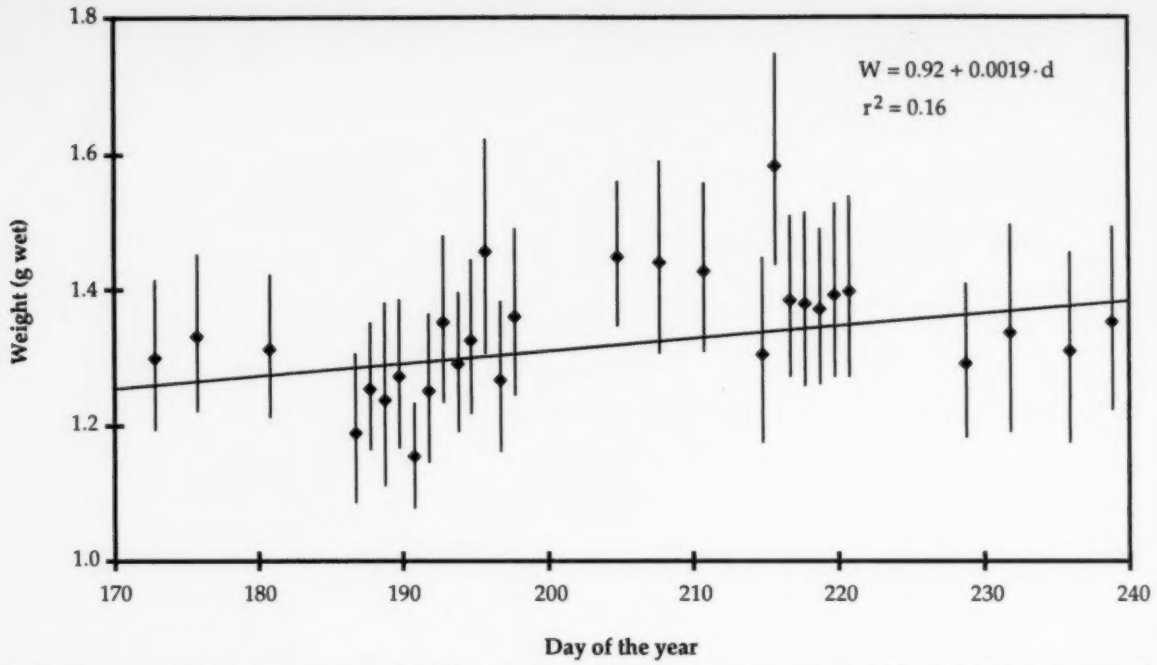

FIG. 1. Observed and fitted growth rate of age 3$^+$ dace from Lake Triton during the summer 1992. The vertical lines represent the 95% CI associated with mean fish weight.

TABLE 2. Average contribution of prey types to the diet of age 3$^+$ dace from Lake Triton during the summer of 1992.

Date	Zooplankton (%)	Aquatic insects (%)
June 29	50	50
July 9	14	86
July 26	16	84
August 2	38	62
August 26	83	17

TABLE 3. Maximum evacuation rates of age 3$^+$ dace (R_{max}), their standard error (SE) and 95% CI, and water temperature (T; °C).

Date	R_{max}	SE	95% CI	T
July 7	0.22	0.05	0.13–0.32	19.4
July 16	0.24	0.04	0.17–0.32	20.4
August 4	0.24	0.04	0.17–0.32	19.3
August 6	0.21	0.04	0.13–0.29	19.0
August 8	0.24	0.05	0.15–0.34	20.3

value (Table 3). It is generally accepted that fish evacuation rates are most directly affected by water temperature (Sharple et al. 1969; Brett and Higgs 1970; Elliott 1972; Persson 1979) and prey type (Thorpe 1974, 1977; Griffiths 1976). In our study, variations in water temperature and food caloric density were small: water temperature was always within 19.8 ± 1.3°C and the caloric density of consumed prey never varied by more than 1%. We also found no significant relationship between evacuation rate and water temperature (Kendall rank correlation; $\tau_5 = 0.74$; $p > 0.05$). We, therefore, assumed that the evacuation rate was constant over the 67-d period and corresponded to the highest R value we estimated ($R = 0.24$; $SE_R = 0.04$). Adoption of the highest R value further minimized the probability that feeding occurred during the time interval selected to estimate R and that our consumption rates underestimated real values.

Consumption Rates

Mean daily ration of dace (back transformed from arcsine) ranged from 1.04 (July 17) to 2.32 g dry wt.·100 g^{-1}·d^{-1} (July 6). The 95% CI around daily ration estimate averaged ±22.1% of the mean values. Mean daily ration varied significantly among sampling dates ($F_{28,1131} = 2.48$; $p < 0.0001$). Cumulative consumption over 67-d estimated using field-derived daily ration was 7.6 kcal and its 95% CI was ±10.4% of the mean value (Fig. 1).

Bioenergetic Model

Cumulative consumption of dace predicted using PS1 averaged 33.5 kcal and overestimated our field value by a factor of 4.4 (Fig. 2). The 95% CI associated with the predicted consumption was 7.1% of the mean value and did not overlap the CI of the observed value. This suggests that the predicted feeding rate obtained using PS1 was significantly different from our direct estimate.

The total quantity of food consumed by dace predicted by PS2 was 6.5 kcal and underestimated our field value by 14.5% (Fig. 1). The 95% CI of the predicted consumption was ±10.0% of the mean value and overlapped the 95% CI of the observed cumulative consumption (Fig. 1), suggesting

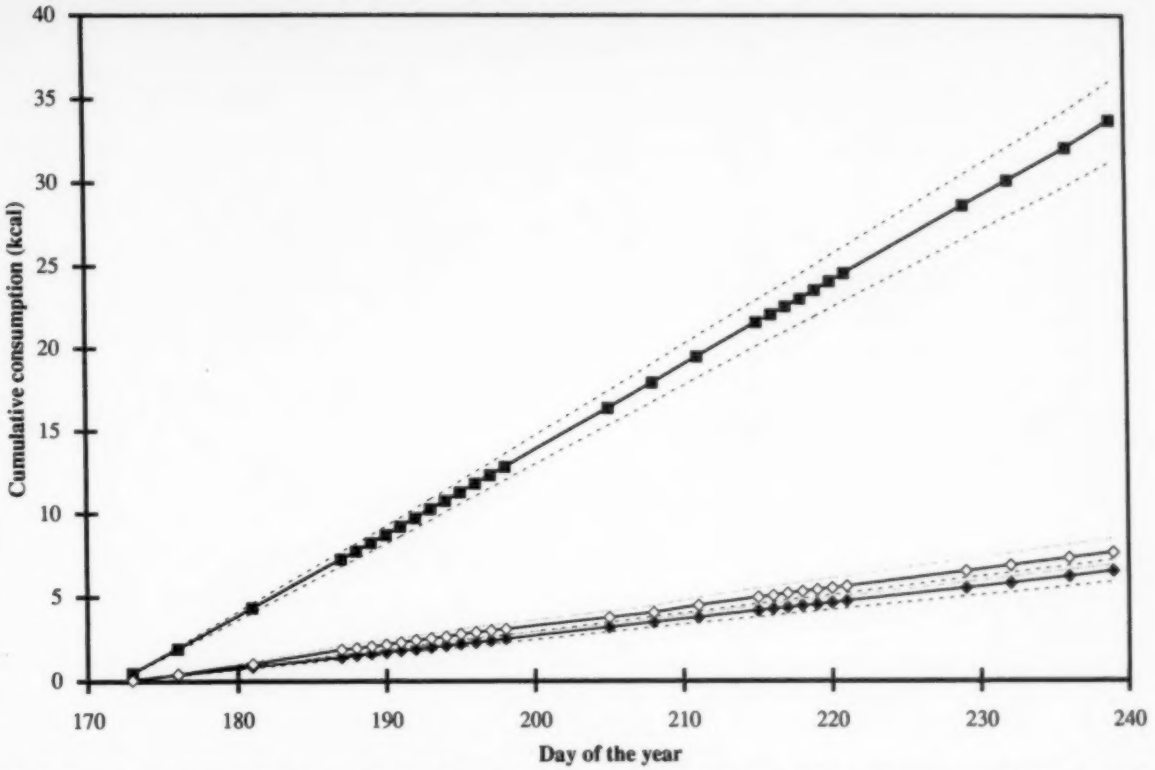

FIG. 2. Cumulative consumption by age 3^+ dace from Lake Triton over a period of 67 d during the summer of 1992. Open diamonds represent field-derived cumulative consumption; solid squares represent the cumulative consumption predicted by the Hewett and Johnson (1987) model; and solid diamonds represent the cumulative consumption predicted by the Hewett and Johnson (1992) model. The broken lines represent the 95% CI associated with cumulative consumption estimates.

that the predicted and observed seasonal consumption rates were not significantly different.

Discussion

Our analyses suggest that the second set of parameters we used to implement the bioenergetic model (PS2) was adequate to estimate the cumulative consumption of dace in the field. The discrepancy between cumulative consumption predicted by the bioenergetic model and the observed value can be explored by the examination and the comparison of the two sets of parameters we used and by the verification of the validity of our field procedure.

Accuracy of Growth Rates

Consumption rates of fish estimated using bioenergetic models require accurate estimation of fish growth rate (Kitchell et al. 1977; Stewart et al. 1983; Rice and Cochran 1984; Hewett and Johnson 1987, 1992). Bias in growth rate estimates could result from size-selective gear or size-selective mortality (Ricker 1975). However, it is our contention that these potential biases were unlikely to influence the estimation of growth rate of dace in our study, and hence, bioenergetic model predictions. Firstly, size-selective gear can bias the estimation of growth rate of fish if small and large individuals of the target population do not have the same probability of being sampled (Green 1979). In our study, the sampling gears (e.g., seine and minnow traps) collected mostly (90%) age 3^+. Because large age 2^+ (5%) and small age 4^+ dace (5%) were also collected by these gears, it is reasonable to assume that small and large age 3^+ dace had the same probability of being captured. Furthermore, because growth rate of age 3^+ dace was estimated using the geometric mean, it was not influenced by extreme sizes of age 3^+ dace that may have been missed by the sampling gears, thus minimizing the influence of the size selectivity of the sampling gears on the growth rate estimate. Secondly, piscivorous fish were absent from Lake Triton, suggesting that size-selective mortality was probably negligible. Finally, although size-selective mortality can influence the estimation of growth rate, substantial errors in consumption estimates are produced only when size-selectivity effects are strong (Cochran and Knutsen 1988). We tested the influence of size-selective mortality on growth rate and cumulative consumption of dace by excluding the lower 50% of the final weight distribution. This procedure represents the highest size-selective mortality observed by Post and Prankevicius (1987) on young-of-the-year yellow perch (*Perca flavescens*) in the field, and hence, represents a worst case scenario for the influence of size-selective mortality on cumulative consumption estimates. Although growth rate was threefold higher (0.006 g wet wt.·d^{-1}) than our original value, cumulative consumption of dace predicted by PS1 and PS2 were

increased by only 1.1- and 1.2-fold, respectively. Furthermore, our field-derived estimate of cumulative consumption was increased by 1.1-fold, counteracting the effect of size-selective mortality on bioenergetic model predictions. Therefore, bias in the estimation of growth rate of dace is unlikely to explain the fourfold difference between the predictions of PS1 and our field value.

Accuracy of Feeding Rates

Inadequate estimation of fish feeding rates could explain the discrepancy between observed and predicted consumption rates (Diana 1983; Carline 1987; Hewett et al. 1991). Three factors could influence the observed values of cumulative consumption rates: (1) the validity of our estimates of gut fullness indices, (2) the accuracy of our evacuation rates, and (3) the efficiency of our approach to extrapolate daily consumption rates to a time scale of 67 d.

Gut fullness indices of a fish from a given population have been shown to vary principally with time of day (Boisclair and Leggett 1988). Consequently, our sampling was planned to collect 10 fish at 6-h intervals. This sampling size and interval has repeatedly been shown to be adequate to estimate fish daily ration using the Eggers model (Boisclair and Leggett 1988; Boisclair and Marchand 1993). We, therefore, believe that our sampling schedule was appropriate to represent average gut fullness values and their associated variations.

Accurate evacuation rates are needed to estimate daily feeding rates of fish (Ney 1990, 1993). Fish evacuation rate is principally affected by water temperature (Sharple et al. 1969; Brett and Higgs 1970; Elliott 1972; Persson 1979) and prey type (Thorpe 1974, 1977; Griffiths 1976). In our study, we estimated the evacuation rate of dace from the decline of the digestive tract content during the feeding cycles. This approach has the advantage that the evacuation rate is estimated at the temperature experienced by the fish and using the prey consumed by the fish in the field. Fish were assumed not to be feeding during the interval when the evacuation was estimated. We maximized the probability of satisfying this assumption by selecting the highest evacuation rate value observed during our study and by using that value to estimate consumption rates for all sampling dates. The evacuation rate estimated using that procedure was similar to values obtained for other minnow species (Boisclair and Leggett 1985; D. Boisclair, unpublished data). For instance, the highest evacuation rate obtained by Boisclair was $0.22 \cdot h^{-1}$, while the evacuation rate of dace estimated in this study was $0.24 \cdot h^{-1}$. The similarity between these values supports our assumption that fish feeding was minimal during the time interval used to estimate fish evacuation rate.

Field cumulative consumption of dace was estimated by integrating daily to weekly survey of gut contents and evacuation rates over time. It has been suggested that this approach can introduce large errors in seasonal or yearly consumption estimates (Smagula and Adelman 1982; Diana 1983). However, we recently showed that food consumption rates of dace in the field did not vary substantially over consecutive days and that cumulative consumption was not affected by sampling intervals that ranged from 1 to 30 d (Trudel and Boisclair 1993). Therefore, the bias related to day to day variation in the quantity of food consumed by fish may not be important in our study.

Heat Increment, Fecal Losses, and Urinary Losses

Heat increment, fecal losses, and urinary losses are generally assumed to represent constant fractions of consumption rates (Brett and Groves 1979; Hewett and Johnson 1987, 1992). Several studies reported that bioenergetic models are not very sensitive to these parameters (Kitchell et al. 1977; Stewart et al. 1983; Bartell et al. 1986; Cui and Wootton 1989). Furthermore, although heat increment, fecal losses, and urinary losses can vary with temperature and food type (Soofiani and Hawkins 1985; Beamish and Trippel 1990), their sum is nearly constant (Kitchell et al. 1977; Bartell et al. 1986; Boisclair and Leggett 1989), and always represented 55% of the feeding rates in our study. Therefore, errors associated with the parameter values of heat increment, fecal losses, and urinary losses may have a relatively small impact on the predictions of the bioenergetic model of dace.

The only major difference between most bioenergetic models and the one we used for dace is the importance of fecal losses. It was assumed that fecal losses represented 40% of the consumed energy, which is higher than most published values for that component. Fecal losses for fish feeding on invertebrates typically range from 10 to 30% of the energy budget (Brett and Groves 1979). However, three points suggest that fecal losses of dace may be higher than most species. First, the evacuation of the complete digestive tract was faster than most benthivorous and planktivorous species. For instance, the evacuation rate of yellow perch (*Perca flavescens*) and of pumkinseed (*Lepomis gibbosus*) fed on shell-free invertebrates at 20°C have been shown to be respectively 0.10 and $0.11 \cdot h^{-1}$ (Boisclair and Leggett 1985, 1988; Boisclair and Marchand 1993). The value we found for dace was $0.24 \cdot h^{-1}$. Second, food was found near the end of the gut 10 min following the meal given to dace that had been starving for 2 d (M. Trudel and D. Boisclair, unpublished data). Finally, dace do not possess a distinct stomach and intestine. Stomachless fishes lack important gastric fluids for digestion, such as HCl and pepsin (Fänge and Grove 1979); therefore, dace may not be efficient in processing food. These results suggest that fecal losses should be important for dace and that a value of 40% of the quantity of food consumed by dace may be appropriate.

Standard Metabolic and Activity Rates

The major difference between the two sets of parameters we used to estimate cumulative consumption rates concerns the costs associated with standard metabolism. SMR estimated using PS1 is approximately 60% higher than the corresponding value determined using PS2. While we believe that the difference can be attributed to disparate methods, this point is difficult to assess because of the lack of information regarding the experimental protocol used to estimate the parameters of PS1.

The model of SMR of PS2 was derived using experiments performed by Winberg (1956), Mann (1965), and Cui and Wootton (1988, 1989). Whether any of these experiments are comparable or can truly represent SMR is debatable. For instance, the fish used by Winberg (1956) and by Mann (1965) were fed and probably displayed energy expenditures associated with activity. The experimental design used by Mann (1965) involved fish kept in an environment of rapid current. Similarly, Cui and Wootton (1988, 1989) estimated SMR from weight loss of starving fish assuming that spontaneous activity was negligible. However, spontaneous

activity metabolism (SMR + A) of unfed fish can be 8–180% higher than SMR (Beamish 1964; Muir and Niimi 1972; Morgan 1973; Krohn and Boisclair 1994). Consequently, these models of SMR may not be adequate because they include energy expenditures associated with heat increment and spontaneous activity. Adequate values of SMR could be determined by subtracting heat increment and spontaneous activity costs from the SMR values estimated using PS2. Unfortunately, heat increment and spontaneous activity costs during Winberg (1956), Mann (1965), and Cui and Wootton (1988, 1989) experiments are not known. Interestingly, Mann (1965) noted that oxygen consumption of dace kept in a rapid water current was 42% higher than the respiration of fish kept in a slow current. This difference, together with the average energy expenditure associated with the heat increment (15–23% of respiration; Boisclair and Leggett 1989), suggests that the true SMR might be 60% lower than the values estimated using PS2. Since PS2 defines activity as a multiple of SMR, a 60% decrease in estimates of SMR requires an adjustment of the activity multiplier. A reanalysis of our data indicates that a 60% reduction of the intercept for maximum standard respiration (to RA = 0.006) combined with an increase in the activity multiplier to 3 resulted in a perfect fit between predicted and observed cumulative consumption rates.

The problem associated with the assumption of fish activity rates may, therefore, not be the use of a constant activity multiplier within one lake but the selection of the appropriate activity multiplier for a given lake characterized, during a defined time interval, by a specific combination of environmental conditions (Boisclair and Leggett 1989). It has been suggested that fish activity could be influenced by water temperature (Lemons and Crawshaw 1985), food consumption (Kerr 1971a, 1982; Boisclair and Leggett 1989; Boisclair 1992), prey abundance and size (Kerr 1971b; Ware 1975), fish abundance (East and Magnan 1987; Boisclair and Leggett 1989), and reproductive status (Koch and Wieser 1983). Despite the potential variability of activity rates (Boisclair and Leggett 1989) there is currently no model or objective criteria available to select a priori an activity multiplier under a given set of environmental conditions. Clearly, much remains to be done to determine the relationship between activity rates and environmental conditions.

As illustrated by the reanalysis of our data, adequate representation of activity rates in bioenergetic models is complicated by the availability of SMR models that are truly "standardized" (fed versus unfed fish displaying different levels of activity). SMR has usually been estimated either from the intercept of the relationship between oxygen consumption and swimming speed (Brett 1964; Beamish 1970; Fry 1971; further referred to as the "intercept" approach) or from the oxygen consumption of fish exhibiting low levels of activity (Diana 1983; Cui and Wootton 1988; Forstner and Wieser 1990; further referred to as the "low activity" approach). The intercept approach has been criticized because respiration rates derived using this approach are never observed experimentally (Forstner and Wieser 1990). However, it is important to note that the low activity approach is also subject to methodological problems. Many empirical and experimental studies have shown that aquaria size and fish abundance may influence fish respiration via their influence on the complexity of swimming patterns (Boisclair and Tang 1993; Tang and Boisclair 1993; Krohn and Boisclair 1994). Consequently, SMR values estimated using the low activity approach may vary with aquarium size, fish size relative to aquarium size, and the number of fish in the respirometers. This situation may, therefore, complicate the estimation of standardized SMR using the low activity approach. While we agree with the criticism directed toward the intercept approach, we also believe that the advantages of obtaining truly standardized SMR using this approach largely outweigh the technical problems associated with its direct measurement.

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Introduction: Multiple Trophic Level Comparisons of Lakes Michigan and Ontario

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The task of documenting food-web interactions in the St. Lawrence – Great Lakes is a daunting one, yet such studies are integral to the management of such spatially and temporally complex systems (Hartig et al. 1991). The sheer physical size of the lakes necessitates a large commitment of research vessel time and scientific personnel to achieve reasonable spatial sampling coverage, and operating costs typically limit the seasonal and interannual sampling resolution for a given lake. To overcome some of these limitations we have been using a team approach to study food-web structure and energy processing in the Great Lakes. Our program includes studies of whole lakes, multiple trophic levels (Sprules et al. 1991), spatially extensive sampling grids (Munawar et al. 1987), seasonal and annual sampling frequencies, new technologies such as bioacoustics for fish (Brandt et al. 1991) and an optical plankton counter for zooplankton (Sprules et al. 1992), multiple whole-system modelling techniques such as geographic information systems (Goyke and Brandt 1993), particle-size models (Sprules et al. 1991), fish growth models (Stewart and Ibarra 1991; Jones et al. 1993), and cross-lake comparisons. This research program provides data on spatial and temporal dynamics of food webs in individual lakes and the opportunity to compare these dynamics among lakes for greater insight into the roles of community configuration, physical processes, and management practices on the structure and production of food webs.

The following papers illustrate this approach by comparing food webs in Lakes Michigan and Ontario. They form part of a group of papers originally presented in a session entitled "Trophic transfer and production dynamics of Lakes Michigan and Ontario" held at the 1993 annual meeting of the International Association of Great Lakes Research in De Pere, Michigan. Authors were asked to include data on both lakes and to make a comparison of the lakes an explicit part of their analysis.

Lakes Michigan and Ontario are similar in mean depth, trophic status, predominance of diatoms in the phytoplankton, presence of exotic invaders (e.g., sea lamprey, alewife, dreissenid mussels, *Bythotrephes cederstroemi*) and the existence of salmonid stocking programs. However, Lake Michigan is about three times larger than Lake Ontario by area and volume, and the spring thermal bar only forms in the south instead of lakewide as in Lake Ontario; Lake Michigan receives half the amount of phosphorus through annual loadings, supports twice the chlorophyll per unit phosphorus, has much higher silica utilization rates, contains more bacteria but fewer autotrophic picoplankton, has larger bodied zooplankton, and has a much lower salmonid stocking rate on an areal basis. In addition, Lake Michigan contains three species of pelagic planktivores; the native bloater (*Coregonus hoyi*), and the exotic alewife (*Alosa pseudoharengus*) and rainbow smelt (*Osmerus mordax*), whereas Lake Ontario contains only the latter two.

During the recent past, community dynamics in the two lakes have been different as well (Hartig et al. 1991). After a precipitous decline in the Lake Michigan alewife population in the early 1980s, bloater replaced them as the dominant planktivore, large-bodied *Daphnia* increased in abundance, and there were changes in seasonal phytoplankton dynamics (Scavia et al. 1987). By contrast, changes in the Lake Ontario food web during the 1980s were minor, and Hartig et al. (1991) speculated that physical and biological differences between the two lakes might result in a different response of Lake Ontario to the nutrient reductions and stocking increases that apparently induced the Lake Michigan changes. By the late 1980s, however, there were growing indications (high salmonid stocking rates, gradually reducing nutrient loadings, declining smelt abundances) that food-web changes in Lake Ontario might be imminent (Hartig et al. 1991). These changes did indeed occur in 1992–1993 when the alewife and smelt populations declined precipitously and salmonid stocking rates were immediately reduced by 50% (Lake Ontario Committee 1992). Our trophic analyses of Lake Ontario just prior to this perturbation indicated a lakewide shortage of primary and secondary production for the smelt and alewife, and excessive salmonid predation on these planktivores (Lake Ontario Committee 1992).

Why did major food-web change occur in Lake Michigan 10 yr before Lake Ontario? Will Lake Ontario respond to the loss of alewife in the same way? If reduced nutrient loadings to the lakes contributed to planktivore declines, one would expect recent Lake Ontario nutrient concentrations to be similar to those in Lake Michigan in the early 1980s. Johengen et al. (1994) show, however, that annual phosphorus loads and chlorophyll and phosphorous concentrations were all higher in Lake Ontario in the early 1990s than they were in Lake Michigan near the time of the alewife collapse.

By contrast, seasonal silica availability and associated diatom production is much more restricted in Lake Ontario (Johengen et al. 1994) and may account for differences in energy provided by lower trophic levels in the two lakes. Millard and Sager (1994) contrast effects of phosphorus control on photosynthesis and light extinction in Green Bay (Lake Michigan) and the Bay of Quinte (Lake Ontario), but it is not clear how events in these embayments could contribute to the 10-yr separation of food-web changes in the two lakes. Using bioenergetic growth models and experimental measurements of feeding rate, Johannsson et al. (1994) show that daily energy requirements of *Mysis relicta* are higher in Lake Ontario than in Lake Michigan and that at certain times of the year Lake Ontario mysids consume so much zooplankton that they may compete with planktivorous fish. In the last paper, Sprules and Goyke (1994) use size-based models of biomass and production to show that the food webs of the two lakes are broadly similar, but that Lake Ontario in 1990 had smaller bodied zooplankton and much greater fish biomass than Lake Michigan in 1987. This configuration parallels that of the Lake Michigan food web just before it went through massive change in the early 1980s, and, as it transpired, preceded a similar transformation of the Lake Ontario community.

When the features of Lake Michigan are compared with those of Lake Ontario (higher nutrient loads and phosphorus concentrations, greater responsiveness of the Bay of Quinte to phosphorus controls, greater caloric demands of *Mysis*, higher planktivore biomass and piscivore stocking rates, and fewer planktivore species) one would have expected food-web perturbations in Lake Ontario to have occurred at the same time they did in Lake Michigan, or even before. That they did not suggests a resilience to change in the Lake Ontario food web that is not yet fully understood, but that is more likely to be revealed through the multiple trophic level analyses illustrated in the following papers.

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Temporal and Seasonal Trends in Nutrient Dynamics and Biomass Measures in Lakes Michigan and Ontario in Response to Phosphorus Control

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Johengen, T.H., O.E. Johannsson, G.L. Pernie, and E.S. Millard. 1994. Temporal and seasonal trends in nutrient dynamics and biomass measures in Lakes Michigan and Ontario in response to phosphorus control. Can. J. Fish. Aquat. Sci. 51: 2570–2578.

Results from long-term ecological monitoring studies on Lake Michigan (1983–92) and Lake Ontario (1981–92) were compared with regard to changes in phosphorus loads. In Lake Ontario, total phosphorus (TP) loads decreased from 14 000 $t \cdot yr^{-1}$ in 1970 to 7500 $t \cdot yr^{-1}$ in 1981, and correspondingly, midlake TP concentration decreased from 25 to 16 $\mu g \cdot L^{-1}$. From 1981 to 1991 TP loads remained around 7500 $t \cdot yr^{-1}$; however, TP concentration continued to decline from 16 to 10 $\mu g \cdot L^{-1}$. Similarly, mean summer particulate organic carbon (POC), chlorophyll *a* (CHL*a*), and nitrate utilization rate decreased by approximately 40, 20, and 50%, respectively. Conversely, silica utilization rates increased markedly after 1983. In Lake Michigan, TP loads also decreased by around 50% from 1974 to 1990 (2000 $t \cdot yr^{-1}$); however, TP concentrations at our 100-m station in the southern basin increased during the study period from around 4 to 8 $\mu g \cdot L^{-1}$. There were no distinct trends in CHL*a* or nutrient utilization patterns; however, POC levels decreased sharply after 1987. Overall, silica utilization rates in Lake Michigan were 50% higher than in Lake Ontario (14.7 vs. 9.6 $\mu g \cdot L^{-1} \cdot d^{-1}$), whereas nitrate utilization rates were only half (1.4 vs. 4.1 $\mu g \cdot L^{-1} \cdot d^{-1}$).

Les résultats de travaux de surveillance écologique à long terme sur le lac Michigan (1983–92) ainsi que sur le lac Ontario (1981–92) ont été comparés de manière à mettre en évidence les changements dans les charges de phosphore. Dans le lac Ontario, la charge en phosphore total (PT) est passée de 14 000 $t \cdot an^{-1}$ en 1970 à 7500 $t \cdot an^{-1}$ en 1981; parallèlement, la concentration en PT à mi-profondeur du lac est passée de 25 à 16 $\mu g \cdot L^{-1}$. De 1981 à 1991, la charge en PT est restée stationnaire, autour de 7500 $t \cdot an^{-1}$; cependant, la concentration en PT a continué de s'abaisser pour passer de 16 à 10 $\mu g \cdot L^{-1}$. De la même manière, la teneur moyenne estivale en carbone organique particulaire (COP) ainsi qu'en chlorophylle *a* (CHL*a*) et le taux d'utilisation des nitrates ont diminué d'environ 40%, 20% et 50%, respectivement. À l'inverse, le taux d'utilisation du silicium s'est accru de manière prononcée après 1983. Dans le lac Michigan, la charge en PT a aussi diminué d'environ 50% entre 1974 et 1990 (2000 $t \cdot an^{-1}$). Toutefois, la concentration en PT à notre station de 100 m dans le bassin sud s'est accrue durant la période d'étude pour passer de 4 à 8 $\mu g \cdot L^{-1}$. On n'a pas décelé de tendance distincte dans la concentration en CHL*a* ou dans l'utilisation des éléments nutritifs; cependant, la teneur en COP a diminué abruptement après 1987. Au bilan, le taux d'utilisation du silicium dans le lac Michigan était 50% supérieur à celui du lac Ontario (14,7 contre 9,6 $\mu g \cdot L^{-1} \cdot jour^{-1}$), alors que le taux d'utilisation des nitrates n'était que de moitié (1,4 contre 4,1 $\mu g \cdot L^{-1} \cdot jour^{-1}$).

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It has been over 20 yr since the Canadian and United States governments created the 1972 Great Lakes Water Quality Act (GLWQA) in response to accelerated eutrophication within the Great Lakes. Since that time, a great deal of effort has gone into controlling phosphorus input to the lakes, which was identified as the primary cause of the eutrophication (Vollenweider 1968; Shapiro 1970; Schelske and Stoermer 1971). A review of earlier monitoring results (DePinto et al. 1986; Stevens and Neilson 1987) revealed that phosphorus control programs achieved significant loading reductions, and that the lakes responded to these reductions in terms of decreased phosphorus and chlorophyll concentrations.

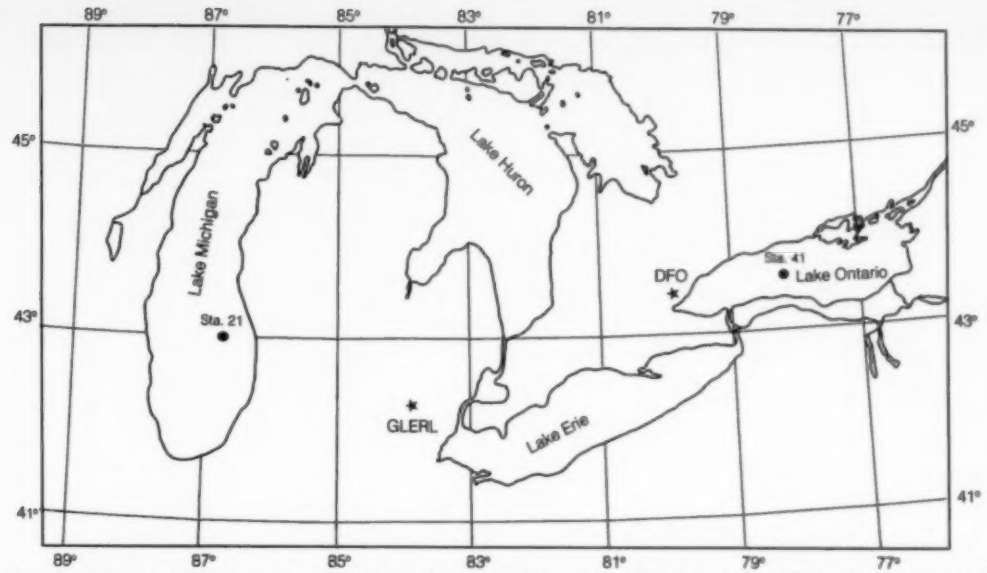

FIG. 1. Station locations for the long term ecological monitoring studies conducted by the Department of Fisheries and Oceans and the NOAA – Great Lakes Environmental Research Laboratory.

In general, however, previous monitoring studies have not been conducted with sufficient temporal intensity and duration to evaluate changes in nutrient dynamics and the response of lower trophic levels to the changes in phosphorus loadings or other natural perturbations.

We discuss the results of two long-term ecological monitoring studies conducted on Lakes Michigan and Ontario since 1983 and 1981, respectively. In both studies detailed information was collected on nutrient dynamics and planktonic community structure and abundances. These monitoring programs were developed by the Department of Fisheries and Oceans (Canada) and the Great Lakes Environmental Research Laboratory (United States) in response to the 1978 GLWQA amendments, which recognized that intensive biological monitoring was required to assess changes in the health or trophic status of lake ecosystems (Johannsson et al. 1985). The monitoring studies were designed to (1) establish detailed information on seasonal and annual trends in the physical, chemical, and biological components of the ecosystem and (2) examine the relationships and interactions among these parameters to interpret and predict changes in community structure and function. Here, we compare and contrast seasonal patterns and long-term trends in nutrient concentrations, nutrient utilization, and measures of biological activity in Lakes Ontario and Michigan, and relate these findings to changes in phosphorus loadings.

Materials and Methods

Both monitoring programs sample only a single offshore station to focus resources on temporally intensive sampling. Previous studies (Rousar 1973; Kwiatkowski 1985) have shown that sampling on temporal scales of 1–2 wk is required to adequately describe seasonal patterns in nutrient dynamics and plankton communities. In both programs, sampling occurred from approximately mid-March through November (Table 1). Details of each sampling program are discussed below.

TABLE 1. Sampling periods (days of the year) and number of cruises conducted for the long-term ecological monitoring programs on Lakes Michigan and Ontario by the Great Lakes Environmental Research Lab, Ann Arbor, Michigan, and the Department of Fisheries and Oceans, Burlington, Ontario, respectively.

	Sampling period		No. of cruises	
Year	Michigan	Ontario	Michigan	Ontario
1981		90–259		22
1982		91–278		22
1983	136–217	96–279	8	24
1984	141–236	94–289	7	24
1985	99–212	94–288	8	25
1986	86–297	100–252	11	20
1987	98–303	104–259	11	21
1988	97–306	98–280	11	21
1989	81–335	94–270	10	22
1990	90–321	93–255	15	20
1991	106–312	93–276	8	21
1992	98–337	91–282	10	22

Lake Ontario Biomonitoring Program

In the Lake Ontario biomonitoring program, sampling was conducted weekly at a midlake station (station 41) located 28 km offshore (43°43′N, 78°01′W) in approximately 130 m of water (Fig. 1). Neilson and Stevens (1986) statistically derived zones in Lake Ontario for homogeneous nutrient and chlorophyll conditions. According to their findings, conditions at station 41 are representative of the large zone of offshore water. A comparison of nutrient and plankton community structure in 1981 and 1982 at an offshore station south of Toronto with that at station 41 further supported the extent of the offshore zone (Johannsson et al. 1985).

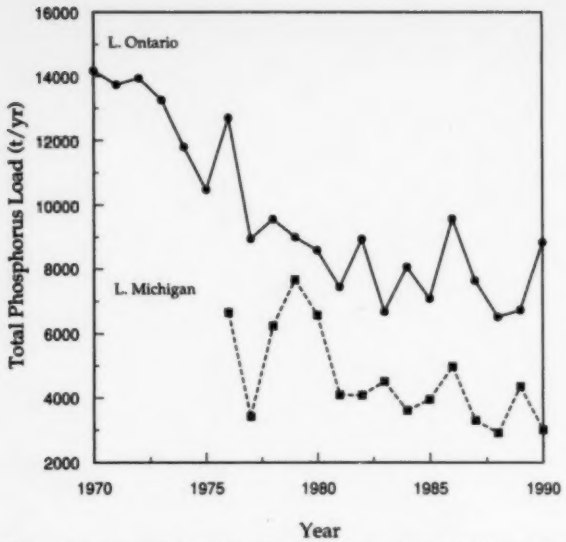

FIG. 2. Total phosphorus loads ($t \cdot yr^{-1}$) to Lakes Michigan and Ontario from 1970 to 1990 as compiled by the International Joint Commission.

Sampling protocol was determined by the thermal structure of the water column. Samples were collected from the surface to 20 m during unstratified conditions, and from surface to 1 m above the thermocline (to a maximum of 20 m) during stratification. Temperature profiles were measured by electronic bathythermograph (BT) and the mixed depth was determined by a density gradient criterion of 0.08 $kg \cdot m^{-3} \cdot m^{-1}$.

Water was collected from the specified depth range using an integrating sampler and subsampled for phytoplankton, particulate organic carbon (POC), chlorophyll *a* (uncorrected for phaeopigments) (CHL*a*), total phosphorus (TP), dissolved silica (SiO_2), and nitrate + nitrite nitrogen (NO_3).

Nutrients were determined on an autoanalyzer system using standard colorimetric procedures. TP was determined by the stannous chloride method after acid persulfate digestion of the sample. CHL*a* was determined after extraction in 90% acetone according to the method of Strickland and Parsons (1968). POC was determined on material retained on a precombusted GF/C filter using a Hewlett-Packard CHN analyzer. Phytoplankton were preserved with Lugol's solution and enumerated using the Utermohl technique. All analytical methods are described in detail in Johannsson et al. (1985). TP concentrations are reported as micrograms P per litre, NO_3 concentrations are reported as milligrams N per litre, and silica concentrations are reported as milligrams SiO_2 per litre.

Lake Michigan Monitoring Program

The ecological monitoring program for Lake Michigan was not formally established at the Great Lakes Environmental Research Laboratory until 1988; however, previous sampling efforts at the same station were conducted with enough frequency and similarity in methods that for some parameters the monitoring record could be extended back to 1983 (Table 1). SiO_2 and NO_3 were not determined regularly during 1985 through 1987 and have been omitted for these years. Since 1988, sampling was conducted approximately biweekly from April to October at station 21, located 26 km offshore (43°1′N, 86°37′W) in 100 m of water (Fig. 1).

During each cruise the water column was sampled at 8–12 discrete depths, using 5-L Niskin bottles, according to the thermal structure of the water column. Temperature profiles were determined by BT. The mixed-layer depth was defined by maximum temperature change within the thermocline. Samples were processed for the same chemical and biological parameters described above for Lake Ontario. Nutrients were determined on an autoanalyzer system using the same colorimetric procedures for NO_3 and SiO_2. TP determinations, however, were made using the molybdate – ascorbic acid colorimetric method after the persulfate digestion. CHL*a* was determined fluorometrically on ground GF/F filters extracted in 90% acetone. POC was determined on an Oceanography International carbon analyzer after persulfate digestion. Details of the analytical procedures are given in Laird et. al. (1987). To allow comparisons to Lake Ontario's integrated sample, epilimnetic concentrations were determined as the mean of samples taken from depths between 0 and 20 m (N = 2–4).

Data Analysis

To compare annual trends within the two lakes, data were reduced to mean values for spring and summer seasonal periods. Spring values are the means from the first sampling trip (usually late March) until the beginning of stratification. For Lake Ontario, summer values are the means of samples collected 18 d after stratification began until the mixed depth exceeded 20 m (early October). For Lake Michigan, sampling was not frequent enough to omit this transition period and summer values are the means of samples collected from the beginning of stratification through the first week of October. Correlation and regression analyses were conducted on the annual spring and summer means for each lake to evaluate relationships among measured physical, chemical, and biological parameters.

To compare seasonal patterns in nutrient and chlorophyll concentrations between the lakes, data were compiled in monthly means for the entire period of record. This procedure was used to minimize the effect of annual and climatic variability, which can greatly alter patterns in nutrient and trophic dynamics for any single year. Lastly, yearly estimates of net SiO_2 and NO_3 utilization rates were derived from linear regressions of concentration versus time. Rates were calculated for the period when concentrations decreased at the maximum rate. In Lake Michigan, the periods of maximum NO_3 and SiO_2 utilization were synchronous, whereas in Lake Ontario maximum NO_3 utilization occurred several weeks later in the season than SiO_2. Consequently, two NO_3 utilization rates were determined for Lake Ontario. One rate represents the maximum utilization rate for the year and a second rate was calculated for the same period of time used in the SiO_2 rate determination.

Results

Annual Trends for Nutrients and Biomass Indicators

Phosphorus loading rates to both lakes were highly variable during the 1980s, but continued to show a general

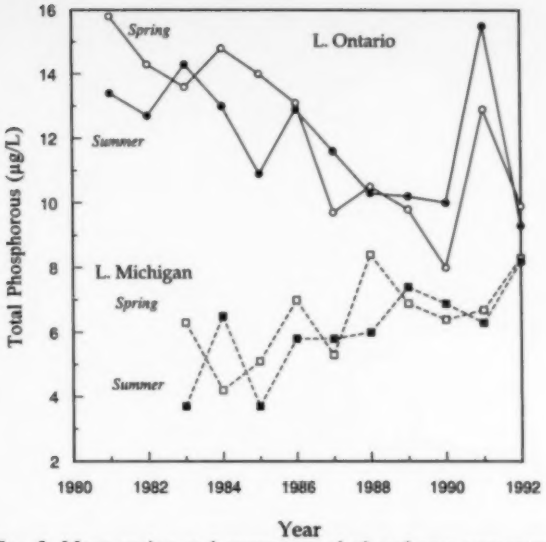

FIG. 3. Mean spring and summer total phosphorus concentrations in Lakes Michigan and Ontario for 1981–92 as determined by the Great Lakes Environmental Research Laboratory and Department of Fisheries and Oceans long term monitoring studies.

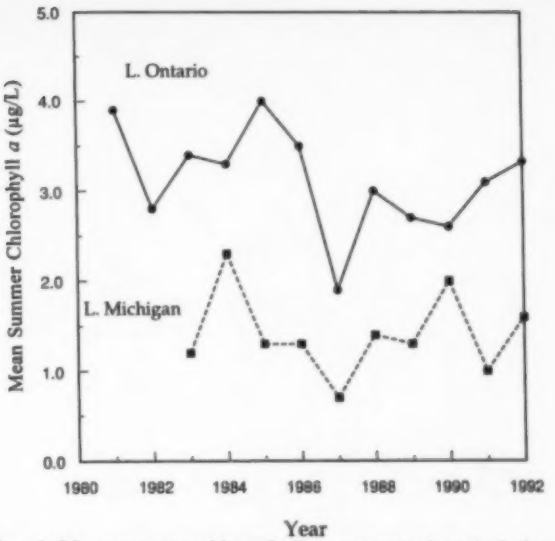

FIG. 4. Mean summer chlorophyll *a* concentrations in Lakes Michigan and Ontario for 1981–92 as determined by the Great Lakes Environmental Research Laboratory and Department of Fisheries and Oceans long term monitoring studies.

decline from previous highs in the early 1970s (Fig. 2). The load reduction in Lake Ontario (8000 $t \cdot yr^{-1}$) was twice that in Lake Michigan (4000 $t \cdot yr^{-1}$). Lake Ontario experienced most of the reduction in loading rates prior to 1977, whereas reductions in Lake Michigan occurred mainly after 1979.

In Lake Ontario, spring and summer TP concentrations declined during the 1980s from 14 and 16 $\mu g \cdot L^{-1}$ respectively, to levels less than 10 $\mu g \cdot L^{-1}$ (Fig. 3). The high TP concentration in 1991 was transitory and presumably not related to present loading rates because levels returned to the 10 $\mu g \cdot L^{-1}$ range within a year. In Lake Michigan, TP concentrations were variable among years, but exhibited an increasing trend from lows of 4 $\mu g \cdot L^{-1}$ in the early 1980s to highs near 8 $\mu g \cdot L^{-1}$ in 1992 (Fig. 3).

Trends in CHL*a* were examined to evaluate whether changes in phosphorus levels affected phytoplankton abundance. Mean summer CHL*a* levels were variable in both lakes (Fig. 4). Summer CHL*a* levels were not correlated with spring TP concentrations in either lake or summer TP concentration in Lake Michigan; however, they were correlated with summer TP concentration in Lake Ontario (Pearson correlation, $r = 0.75$, $p < 0.01$). In Lake Ontario, summer CHL*a* ranged from 1.9 to 4.0 $\mu g \cdot L^{-1}$ but exhibited an overall decline during the study period. The average level from 1987 to 1991 was 23% lower (2.7 vs. 3.5 $\mu g \cdot L^{-1}$) than during 1981–1986. In Lake Michigan, summer CHL*a* varied between 0.7 and 2.3 $\mu g \cdot L^{-1}$, with no apparent trend. The only similarity in CHL*a* trends was that in both lakes minimum values occurred in 1987.

POC was examined as another measure of planktonic biomass. In Lake Ontario, mean summer POC decreased by half from a high of 0.63 $mg \cdot L^{-1}$ in 1981 to 0.31 $mg \cdot L^{-1}$ in 1990 (Fig. 5). Mean summer POC was highly correlated with both mean summer TP ($r = 0.75$, $p < 0.01$) and mean summer CHL*a* concentrations ($r = 0.71$, $p = 0.01$). Lake Michigan also experienced a 50% decrease in mean summer POC

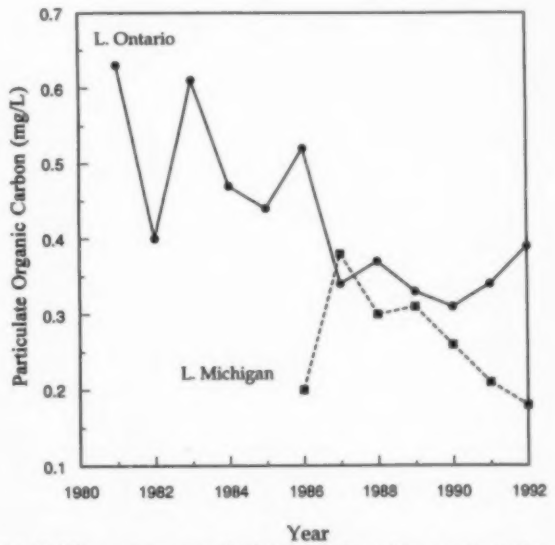

FIG. 5. Mean summer particulate organic carbon concentrations in Lakes Michigan and Ontario for 1981–92 as determined by the Great Lakes Environmental Research Laboratory and Department of Fisheries and Oceans long term monitoring studies.

during the study period. Levels declined from a high of 0.38 $mg \cdot L^{-1}$ in 1987 to a low of 0.18 $mg \cdot L^{-1}$ in 1992. In contrast to Lake Ontario, however, mean summer POC was correlated with neither TP nor CHL*a*.

Seasonal Patterns of Nutrient Use and Chlorophyll *a*

Seasonal patterns in nutrients and chlorophyll concentrations were compared to evaluate differences in phytoplankton

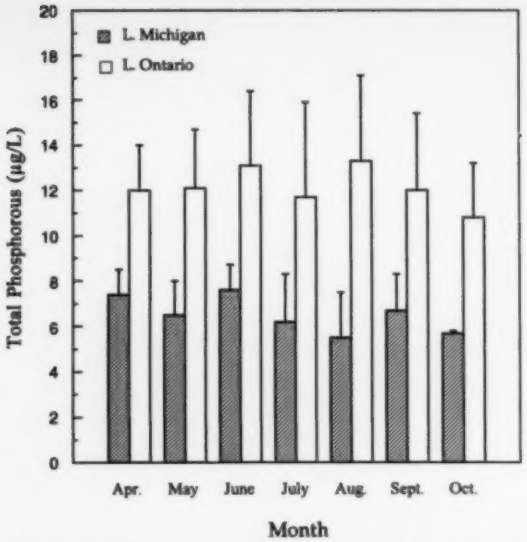

FIG. 6. Seasonal patterns for epilimnetic total phosphorus in Lakes Michigan and Ontario. Lake Ontario monthly means compiled from station 41 data collected from 1981 to 1992. Lake Michigan monthly means compiled from station 21 data collected from 1983 to 1992. Error bars = 1 SD.

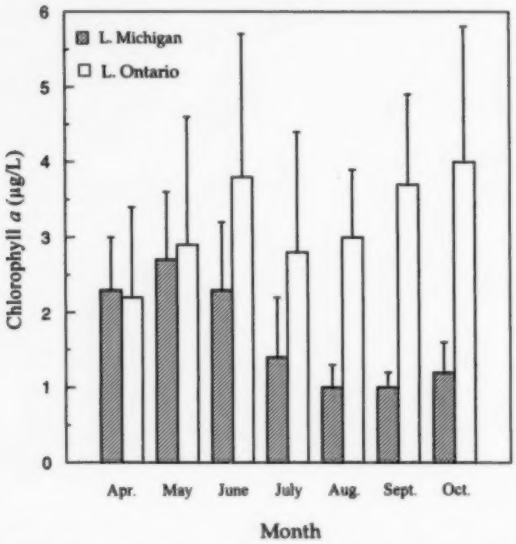

FIG. 7. Seasonal patterns for epilimnetic chlorophyll *a* in Lakes Michigan and Ontario. Data plotted as in Fig. 6.

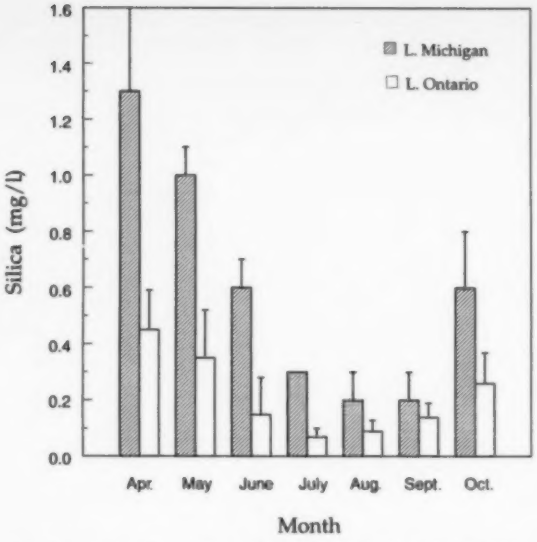

FIG. 8. Seasonal patterns for epilimnetic silica in Lakes Michigan and Ontario. Data plotted as in Fig. 6.

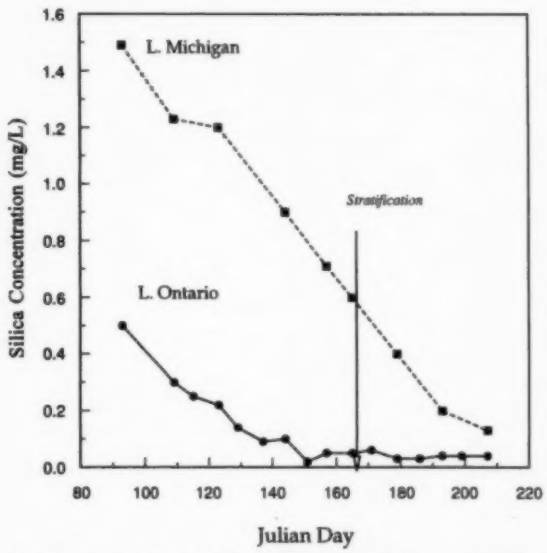

FIG. 9. A time series of 1990 epilimnetic silica concentrations in Lake Michigan (station 21) and Lake Ontario (station 41) during April to August in 1990. Typical date of stratification for both lakes is indicated.

production patterns between the two lakes. TP concentrations showed little seasonal variation in either lake from April to October (Fig. 6). The higher variability in monthly means for Lake Ontario reflects the greater change in concentration during the study. In Lake Ontario, average TP concentrations varied by 2.3 $\mu g \cdot L^{-1}$ during the year, or 20% from the overall mean of 12.1 $\mu g \cdot L^{-1}$. In Lake Michigan, the annual range was 1.9 $\mu g \cdot L^{-1}$, or 29% from the overall mean of 6.5 $\mu g \cdot L^{-1}$.

Seasonal CHL*a* patterns for the two lakes reflect their different trophic status (Fig. 7). Both lakes displayed a bimodal pattern with peaks in spring and fall; however, the timing and magnitude of peaks were quite different. In both lakes, CHL*a* levels were approximately 2 $\mu g \cdot L^{-1}$ in April and increased in May. In Lake Michigan, CHL*a* levels began to decline in June and minimum levels were observed from August through October. During this time, phytoplankton presumably remain phosphorus and silica limited, and are

TABLE 2. Maximum net epilimnetic nutrient depletion rates ($\mu g \cdot L^{-1} \cdot d^{-1}$) for Lakes Michigan and Ontario calculated from linear regressions of concentration vs. Julian day. For Lake Ontario, a nitrate depletion rate was also calculated for the same time period used to determine silica rates. All regressions were significant ($p < 0.05$).

	Lake Michigan			Lake Ontario				
Year	Jul. day	SiO_2	NO_3	Jul. day	SiO_2	NO_3	Jul. day	NO_3
1981				78–181	3.1	2.6	133–208	4.6
1982				152–207	6.5	4.0	152–207	4.2
1983	136–191	13.8	1.4	102–180	5.0	3.2	137–187	6.4
1984	142–187	15.6	1.4	150–177	21.8	7.8	150–177	9.3
1985				120–169	12.0	2.8	141–204	3.0
1986				119–183	9.1	2.0	133–209	3.4
1987				113–161	9.3	2.1	118–210	2.8
1988	132–195	13.2	1.3	127–168	14.5	2.0	147–182	2.9
1989	144–199	13.8	1.5	94–166	5.6	1.0	145–208	3.3
1990	141–190	16.2	1.5	93–151	7.7	0.9	115–193	2.9
1991	148–191	18.5	1.6	114–157	10.9	2.5	121–177	4.5
1992	135–204	12.0	1.4	119–162	9.4	1.2	147–240	2.4
Mean	140–194	14.7	1.4	115–172	9.6	2.7	137–200	4.1
SD		2.2	0.1		5.0	1.9		2.0

also subject to intense grazing by the *Daphnia* community (Scavia and Fahnenstiel 1987). The fall peak may be limited or delayed by the presence of actively growing phytoplankton within a deep chlorophyll layer (Fahnenstiel and Scavia 1987) that trap nutrients within the metalimnion and delay their re-entry into the epilimnion.

In Lake Ontario, CHL*a* continued to increase in June and peaked at much higher levels than in Lake Michigan. Although not reflected (Fig. 7), the timing of the spring peak was much more variable in Lake Ontario and occurred anywhere from May to July for different years. The decline in CHL*a* during the summer was much less severe in Lake Ontario and only lasted through August. CHL*a* levels increased again in September and built to a secondary peak in October similar to that for June. The dramatic fall peak in Lake Ontario results from several factors. The deepening thermocline entrains nutrient-rich metalimnetic water, grazing pressures are reduced as temperatures drop, and there appears to be a buildup of nonedible chlorophytes (Johannsson et al. 1985). Consequently, while both lakes started out with similar CHL*a* values in the spring, by fall, values in Lake Ontario are nearly four-fold greater than in Lake Michigan.

SiO_2 exhibited the most dramatic seasonal cycle of the nutrients (Fig. 8). The pattern reflects rapid utilization of dissolved SiO_2 by phytoplankton and relatively slow recycling rates after incorporation in a biogenic form. The overall seasonal patterns were similar between the two lakes; however, they differed substantially in the timing and magnitude of concentration changes (Fig. 9 and 10). Lake Michigan exhibited an SiO_2 concentration range from 1.4 $mg \cdot L^{-1}$ in the winter to a low of 0.15 $mg \cdot L^{-1}$ in August. In Lake Ontario, the concentration range was much smaller and the time needed to reach minimum levels much shorter. Concentrations were approximately 0.6 $mg \cdot L^{-1}$ in the winter and typically declined to 0.05 $mg \cdot L^{-1}$ by early July. Details of the SiO_2 utilization patterns can be seen in the concentration time series for 1990 (Fig. 9). In Lake Ontario, most of the dissolved SiO_2 pool was removed from the epilimnion prior to stratification (mean = June 15) and concentrations remained very low throughout the entire summer. During

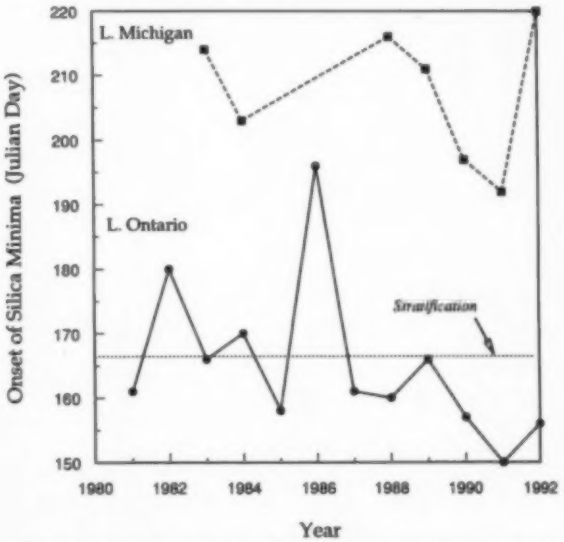

FIG. 10. Yearly estimates of the date when epilimnetic silica concentrations drop below 0.1 $mg \cdot L^{-1}$ for Lake Michigan (station 21) and Lake Ontario (station 41). Typical date of stratification for both lakes is indicated.

the study, the proportion of the dissolved SiO_2 pool removed before stratification ranged from 45 to 97%. In years when less than 70% was removed, a sharp decrease often occurred immediately after stratification. For example, in 1984 the SiO_2 concentration just prior to stratification was still 0.60 $mg \cdot L^{-1}$, but 2 wk later had fallen to only 0.07 $mg \cdot L^{-1}$. In that year, spring diatom abundance was 10% of previous levels. After stratification there was a rapid increase in diatom and chrysophyte biomass, which presumably caused the rapid decrease in SiO_2. In Lake Michigan, SiO_2 concentrations were high enough, and diatom abundance low enough, that only half of the dissolved SiO_2 pool was removed prior to stratification and minimum levels were

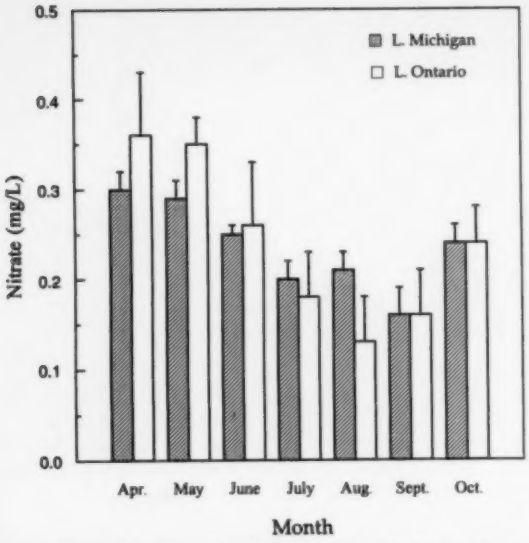

FIG. 11. Seasonal patterns for epilimnetic nitrate in Lakes Michigan and Ontario. Data plotted as in Fig. 6.

not reached until August. The proportion of the SiO_2 pool removed before stratification ranged from only 40 to 60%.

During the study period, the average SiO_2 utilization rate was 55% higher in Lake Michigan than in Lake Ontario (14.7 vs. 9.6 $\mu g \cdot L^{-1} \cdot d^{-1}$) (Table 2). Utilization rates were quite variable in Lake Ontario, however, there was a notable increase after 1983. Increased utilization rates may help explain the subsequent advancement in the onset of minimum SiO_2 concentrations for Lake Ontario (Fig. 10). Excluding 1986, concentrations dropped below 0.1 $mg \cdot L^{-1}$ progressively earlier during the year. By 1990, concentration minima were observed nearly 3 wk earlier in the year than during the early 1980s. In Lake Michigan, minimum SiO_2 concentrations occurred much later in the year than in Lake Ontario (mean day of the year = 208 vs. 165). The timing of concentration minima was quite variable among years and did not exhibit any consistent trend during the study.

NO_3 concentrations in the two lakes were much more similar than for SiO_2 and exhibited similar seasonal patterns (Fig. 11). Again, however, there were differences in the timing and rates of change between the lakes. In Lake Michigan, around 50% of the epilimnetic NO_3 was depleted throughout the year. Mean concentrations ranged from a maximum of 0.31 $mg \cdot L^{-1}$ to a minimum of 0.16 $mg \cdot L^{-1}$. In Lake Ontario, the typical annual NO_3 concentration range was slightly greater going from a winter maximum of around 0.40 $mg \cdot L^{-1}$ down to 0.12 $mg \cdot L^{-1}$.

Average NO_3 utilization rates in Lake Ontario during the study (4.1 $\mu g \cdot L^{-1} \cdot d^{-1}$) were nearly three times those of Lake Michigan (1.4 $\mu g \cdot L^{-1} \cdot d^{-1}$) (Table 2). In Lake Ontario, NO_3 utilization rates calculated for the period of maximum SiO_2 utilization averaged only 2.7 $\mu g \cdot L^{-1} \cdot d^{-1}$, which was still nearly double that for Lake Michigan. NO_3 utilization rates in Lake Ontario declined considerably during the study period, and rates from 1981 to 1984 were generally twice as high as those for 1985–92. Rates in Lake Michigan were very consistent throughout the study.

Discussion

Phosphorus-control programs established under the 1972 and 1978 GLWQA greatly reduced annual phosphorus loads to lakes Michigan and Ontario. The lakes are at or below the International Joint Commission's (IJC) recommended target levels of 5600 and 7000 $t \cdot yr^{-1}$ for Michigan and Ontario, respectively (Fig. 2). Loading rates may already have reached new equilibria and much of the observed variability in rates during the 1980s may have resulted from differences in nonpoint source contributions during wet versus dry years (D.M. Dolan, International Joint Commission, Windsor, ON, personal communication).

Lake Ontario demonstrated a much greater response to changes in phosphorus loading than Lake Michigan; however, the magnitude of load reduction was nearly twice as large (8000 vs. 4000 $t \cdot yr^{-1}$). This difference is even more significant given that load reductions in Lake Ontario should produce about twice the concentration change given their morphological and hydrological differences (Chapra and Sonzogni 1979). The observed loading-concentration response in Lake Ontario agreed very closely with the mathematical models that were used to set initial target loads (see Bierman 1980). Prior to 1974, spring TP concentrations in offshore waters averaged 26 $\mu g \cdot L^{-1}$, but by 1980 concentrations had declined to levels around 16 $\mu g \cdot L^{-1}$ (Kwiatkowski 1982; Stevens 1988). TP concentrations continued to decline throughout the 1980s and are presently below the recommended level of 10 $\mu g \cdot L^{-1}$ deemed necessary to restore meso-oligotrophic conditions (Vollenweider 1968).

In Lake Ontario, the response to phosphorus control went beyond just decreased TP concentrations and was observed in changes to CHL*a* and POC as well. Although changes in these variables were not strongly correlated with annual TP trends, notable decreases in both CHL*a* and POC occurred between the first and last half of the 1980s. Furthermore, Kwiatkowski (1982) determined that CHL*a* and POC in the offshore waters of Lake Ontario had declined by 0.8 $\mu g \cdot L^{-1}$ and 0.16 $mg \cdot L^{-1}$, respectively, between 1974 and 1980. The magnitude of these changes is similar to those observed during the 1980s. It is unclear, however, why much of the observed decrease in POC and CHL*a*, and shifts in nutrient utilization, appeared as stepwise changes. The abruptness of these changes suggests that factors other than phosphorus control played important roles and that effects are integrated quickly throughout the lower food web.

Unlike Lake Ontario, water-quality conditions in southeastern Lake Michigan have not responded to observed decreases in phosphorus loading. TP concentrations actually increased at station 21 over the course of the study from a low of 4.2 $\mu g \cdot L^{-1}$ in 1984 to over 8 $\mu g \cdot L^{-1}$ in both 1988 and 1992. This increasing trend is contradictory to earlier monitoring studies by the IJC (1989), which found no significant changes from 1983 to 1987, and to results from a time-dependent phosphorus-loading model (Lesht et al. 1991). It is difficult, however, to compare results with previous studies because of differences in sampling techniques. The IJC study was conducted at different sampling locations only three times a year, and the modeling study was conducted on data retrieved from STORET (U.S. EPA data base) without regard to temporal or spatial conditions. It is unclear whether the observed discrepancies resulted from differences in sampling techniques, or whether water-quality

trends at station 21 are not representative of conditions throughout the lake. TP concentrations did exhibit a great deal of seasonal and annual variability and, perhaps, were more influenced by exchange with coastal waters than previously believed. For example, in 1993, TP concentration increased from around 3.4 $\mu g \cdot L^{-1}$ in April to 8.3 $\mu g \cdot L^{-1}$ in late May after passage of the 4°C thermal front and then returned to levels around 6.0 $\mu g \cdot L^{-1}$ in July (T.H. Johengen, unpublished data). TP values of 8 $\mu g \cdot L^{-1}$ were commonly reported for Lake Michigan during 1979 and 1980 and the occasional occurrence of this level does not indicate that there has been deterioration in water quality. The observed TP trend at station 21 merely suggests that southeastern Lake Michigan has not responded to decreased loads.

Several factors may have contributed to the different response to phosphorus control in the two lakes. One important factor was the magnitude of load reductions in the two lakes. The total phosphorus budget model of Chapra and Sonzogni (1979), predicts that a loading reduction of 7000 t to Lake Ontario would produce a concentration reduction of 14.7 $\mu g \cdot L^{-1}$, nearly identical to the observed change. For Lake Michigan, if we consider only the reduction that occurred to the main lake (i.e., minus Green Bay), loads were reduced by only 2000 t. This loading change would produce a TP reduction of 2.6 $\mu g \cdot L^{-1}$. Spatial and temporal variations may be too large in Lake Michigan to detect this level of change given the present sampling techniques.

A second factor that may have affected the responsiveness of the lakes is the difference in their TP residence times. The time required for Lake Ontario to reach a new steady-state TP concentration, given a reduction in loading, is predicted to be half that for Michigan (10 vs. 20 yr) (Chapra and Sonzogni 1979). Given that the majority of load reduction to Lake Michigan occurred after 1980, it is unrealistic to expect any direct consequences at this time. In Lake Ontario, large reductions in loadings occurred from 1974 to 1980 and the present observations are well within the expected response window.

Lakes Michigan and Ontario also exhibited large differences in their patterns of nutrient utilization. These differences have developed as a result of the accelerated eutrophication of the lower Great Lakes since the 1940s (Schelske 1975). Silica concentrations have become severely depleted in Lake Ontario because phosphorus enrichment stimulated diatom production and led to increased sedimentation of SiO_2 (Schelske et al. 1986).

Net epilimnetic SiO_2 utilization rates were 55% higher on average in Lake Michigan than in Lake Ontario (Table 2). These results appear surprising, given that both diatom abundance and phosphorus concentration are much greater in Lake Ontario; however, several factors may explain the disparity. One reason utilization rates are lower in Lake Ontario (Table 2) appears to be the timing of diatom production. On average, in Lake Ontario, the period of maximum SiO_2 uptake occurred between April 28 and June 21. Consequently, most of the diatom production in Lake Ontario occurred during the prestratified period when colder water temperatures and lower light levels would slow diatom growth. Based on the difference in concentration between winter maxima (approximately 0.6 $mg \cdot L^{-1}$) and that just prior to stratification, between 45 and 97% of the epilimnetic silica pool was removed prior to stratification. In Lake Michigan, maximum SiO_2 uptake was not observed until May 20 and typically extended to July. Based on concentration differences (assuming winter maxima of 1.4 $mg \cdot L^{-1}$), only 40–60% of the epilimnetic SiO_2 pool was utilized prior to stratification. Warmer temperatures and higher mean epilimnetic irradiance levels after stratification should promote higher rates of diatom growth and SiO_2 utilization than during the prestratified period.

A second factor that may explain lower SiO_2 utilization rates in Lake Ontario is that the average SiO_2 concentration on April 28 (the start of the period of maximum utilization) was 0.4 $mg \cdot L^{-1}$, below that considered necessary for optimum diatom growth (Parker et al. 1977). In Lake Michigan, the average concentration at the start of maximum utilization was 1.1 $mg \cdot L^{-1}$.

In both lakes, maximum SiO_2 utilization rates determined during the course of this study were higher than those calculated from earlier seasonal studies in 1969 and 1970. Calculations performed on the data of Rousar (1973) for offshore Lake Michigan indicate that in 1970 maximum SiO_2 utilization rates were around 9.2 $\mu g \cdot L^{-1} \cdot d^{-1}$, compared with the study period average of 14.7 $\mu g \cdot L^{-1} \cdot d^{-1}$. For Lake Ontario, calculations on 1969 monthly mean concentrations data (Shiomi and Chawla 1970) indicate a SiO_2 utilization rate of only 4.3 $\mu g \cdot L^{-1} \cdot d^{-1}$. This value is similar to rates observed in 1981–83, but less than half that of the study period average.

SiO_2 utilization patterns in Lake Ontario changed substantially during the study period. Maximum SiO_2 utilization rates increased sharply after 1983 and there was a marked shift in the onset of minimum silica concentrations (<0.1 $mg \cdot L^{-1}$). Between 1981 and 1992 the onset of minimum concentrations advanced by approximately 3 wk (Fig. 11). This change was presumably caused by the increase in diatom abundance, which averaged almost threefold higher during 1987–91 than during 1981–86 (0.34 vs. 0.97 $g \cdot m^{-3}$). It is not known whether the observed changes in phosphorus levels prompted this recent change in diatom abundance.

Differences in NO_3 utilization rates between the lakes reflect their different trophic status. Maximum utilization rates averaged 2.8 times higher in Lake Ontario than in Lake Michigan. This difference is expected given higher phytoplankton abundances and phosphorus levels in Lake Ontario. NO_3 utilization rates appear to have responded to changes in phosphorus levels within Lake Ontario. NO_3 utilization rates exhibited a decreasing trend throughout the present study period as phosphorus levels continued to decline. However, data from Shiomi and Chawla (1970) indicate that maximum utilization rates in 1969 were around 2.2 $\mu g \cdot L^{-1} \cdot d^{-1}$, or nearly half the 1980's average.

In Lake Michigan, NO_3 utilization rates did not change during the study period, even though there was an apparent increase in TP concentration. Based on the data of Rousar (1973), present day NO_3 utilization rates agree closely with those found in 1970.

Conclusions

Long-term ecological monitoring studies, conducted on time scales of weeks, are required to adequately describe both seasonal and annual changes in nutrient and lower food-web trophic dynamics. Lower trophic levels in Lake Ontario have responded to phosphorus control programs. Changes in phosphorus concentration agree well with those predicted

by models used to set recommended target loads. During the past decade there have been changes in POC, CHL*a*, and nutrient utilization rates, which would suggest that Lake Ontario appears to be shifting towards more meso-oligotrophic conditions.

Southeastern Lake Michigan has not responded to reduced phosphorus loads. The lack of response may in part be due to the magnitude of loading change and the time required to reach a new equilibrium concentration. Additionally, large seasonal and annual variability at the present monitoring station may be masking trends in other parts of the lake.

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Comparison of Phosphorus, Light Climate, and Photosynthesis between Two Culturally Eutrophied Bays: Green Bay, Lake Michigan, and the Bay of Quinte, Lake Ontario

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Millard, E.S., and P.E. Sager. Comparison of phosphorus, light climate, and photosynthesis between two culturally eutrophied bays: Green Bay, Lake Michigan, and the Bay of Quinte, Lake Ontario. Can. J. Fish. Aquat. Sci. 51: 2579–2590.

Trophic status, response to phosphorus control, and the underwater light climate were compared for the major bays of Lake Michigan (Green Bay) and Lake Ontario (Bay of Quinte). The Bay of Quinte has shown the greatest response to phosphorus controls, but conditions were not as eutrophic prior to controls as in Green Bay. There were distinct spatial gradients in trophic indicators (chlorophyll *a* and light extinction) as well as in background light extinction in both bays. Photosynthetic rates remain higher in Green Bay than in the Bay of Quinte, although this is more pronounced for daily photosynthesis per cubic metre at optimal light than for daily rates per square metre. Background light extinction reduced areal photosynthesis in Green Bay because of competition for light absorption between chlorophyll and suspended solids. Potential effects of remedial actions such as reduced phosphorus and suspended loading on phytoplankton photosynthesis were assessed. Lowering chlorophyll would cause a significant decline in areal photosynthesis rates but decreasing background light extinction could lead to higher rates.

On a comparé le niveau trophique, la réponse à la réduction de la charge en phosphore et le régime d'éclairement dans les baies principales du lac Michigan (baie Green) et du lac Ontario (baie de Quinte). C'est la baie de Quinte qui a marqué la réponse la plus accentuée à la réduction de la charge en phosphore, mais les eaux de cette baie étaient moins eutrophes, avant les mesures, que celles de la baie Green. Dans les deux baies, les indicateurs du trophisme (chlorophylle *a* et extinction de la lumière) suivaient des gradients spatiaux distincts, tout comme l'extinction de la lumière au niveau de fond. L'activité photosynthétique reste supérieure dans la baie Green à ce qu'elle est dans la baie de Quinte même si ce phénomène est plus prononcé en termes de photosynthèse quotidienne par mètre cube dans des conditions optimales d'éclairement qu'en termes de photosynthèse quotidienne par mètre carré. L'extinction de la lumière au niveau de fond réduit la photosynthèse mesurée en fonction de la superficie dans la baie Green parce qu'il existe une compétition pour l'absorption de la lumière entre la chlorophylle et les matières en suspension. Les auteurs évaluent les effets possibles de mesures correctives comme la réduction de la charge en phosphore et en matières en suspension sur la photosynthèse phytoplanctonique. La réduction de la teneur en chlorophylle abaisserait considérablement l'activité photosynthétique par unité de surface, mais l'amoindrissement de l'extinction de la lumière au niveau de fond pourrait à l'inverse conduire à une hausse de cette activité.

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Green Bay (GB) and the Bay of Quinte (BoQ) are major near-shore water bodies of Lakes Michigan and Ontario respectively (Fig. 1 and 2). Both these areas have been designated as Areas of Concern (AOCs) by the International Joint Commission because of excessive phosphorus loadings. Remedial Action Plans (RAPs) are currently being developed that will restore beneficial uses and rehabilitate these degraded ecosystems. The similarities of the bays include a history of water-quality problems due to cultural eutrophication, distinct depth and trophic gradients along their lengths, and intensive human use. Reduction in phosphorus inputs have occurred in both ecosystems as part of the remediation process.

The BoQ has been studied by Project Quinte, a multiagency, cooperative research project, and results of the early remediation effects are discussed extensively in Minns et al. (1986a). GB has also had major studies on nutrients, primary and secondary productivity, and trophic interactions. Several studies on GB have utilized the trophic gradient to examine nutrient-related processes and other features of aquatic ecosystems (e.g., Vanderhoef et al. 1974; Richman et al. 1984; Auer et al. 1986; Sager et al. 1988; Sager and

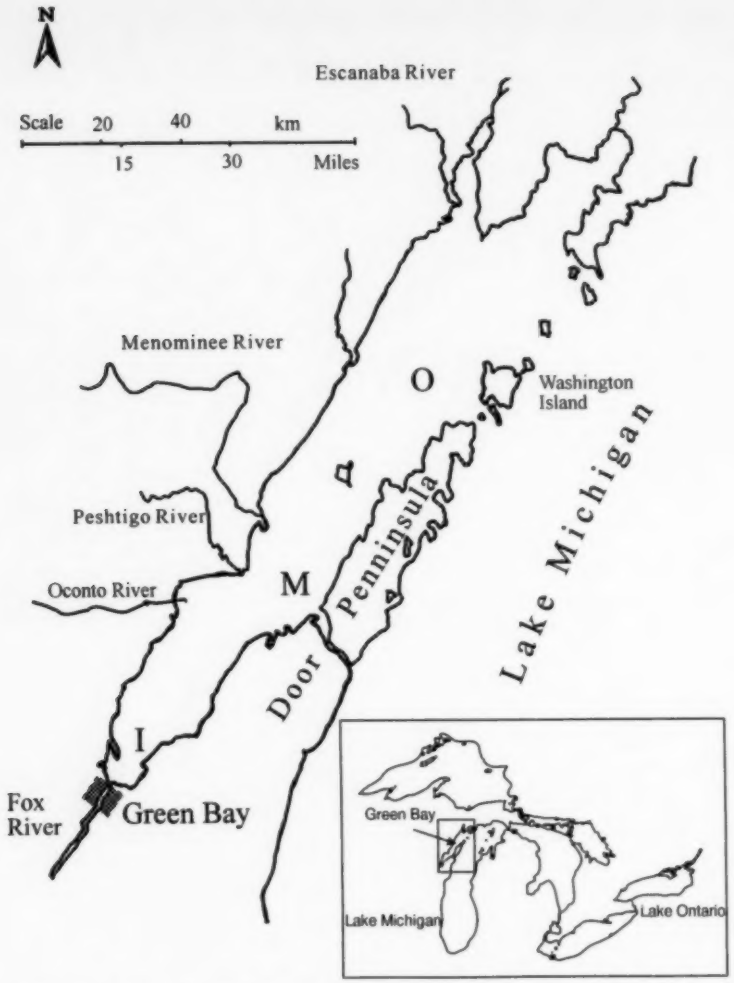

FIG 1. Green Bay showing main tributaries, urban centres, and the location of the sampling stations representing the three main regions of the bay: inner (I), middle (M), and outer (O).

Richman, 1991). The studies in both AOCs arose because of similar nutrient problems but have been independent of one another and were never originally intended for comparison. Consequently, methods and sampling intensities differ between the two studies.

The purpose of our study is to compare the GB and BoQ ecosystems with regard to their morphometry, hydrology, phosphorus loadings, underwater light climate, and phytoplankton photosynthesis rates (PP). The comparison of the two factors most likely to affect phytoplankton growth, light and phosphorus, as well as the response of these two bays to phosphorus loading reductions, may provide insights into the issue of nutrient management in the Great Lakes in general.

Sampling and Methods

Sampling details and methods in BoQ up to 1982 are described in detail in Millard and Johnson (1986). A brief summary is given here with the changes pertinent to the 1991 field season, which has been used for some of the comparisons with GB. Samples were collected weekly up to 1982 and biweekly thereafter at stations representative of the inner, middle, and outer bays (Fig. 2). Composite samples for all nutrient and phytoplankton biomass parameters were collected through a depth of twice the Secchi disc depth as an approximation of the euphotic zone, which is always less than the depth of the epilimnion (Z_m). Phosphorus samples were analyzed by the Ontario Ministry of Environment and Energy (OMEE) laboratory in Toronto following standard methods (American Public Health Association 1985). Long-term reporting of chlorophyll is based on samples collected on Millipore membrane filters (1.2-μm pore size; 1972–84) and on nylon membrane filters (1.2-μm pore size; 1985–present) and analyzed by OMEE using a 24 h, 90% acetone extraction with mild agitation followed by spectrophotometric analysis of the extracts. In 1991, samples for chlorophyll *a* analysis were collected on GF/C filters, ground in 90% acetone, and the extracts analyzed spectrophotometrically (Strickland and Parsons 1972). Chlorophyll

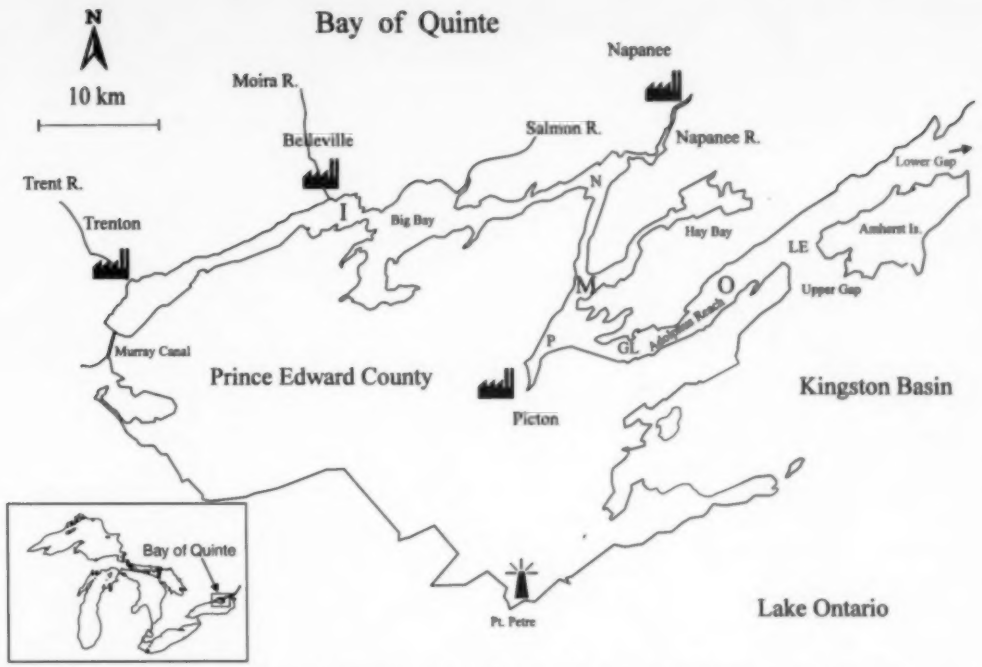

FIG. 2. Bay of Quinte showing main tributaries, urban centres, and location of sampling stations representing the three main regions of the bay: inner (I), middle (M), and outer (O). Other stations in the inner (N), middle (P), and outer (GL, LE) bays are also shown.

values reported here are uncorrected for phaeopigments. Extinction of photosynthetically available radiation (ε_{par}) from profiles of light intensity measured with an underwater quantum sensor (LI-192S, LI-COR Co., Lincoln, NE), was estimated as the slope of a semilogarithmic regression of light intensity as a function of depth. Incident PAR was measured with a quantum sensor (LI-190) and datalogger (LI-1000) positioned on top of the Point Petre lighthouse (Fig. 2).

Least-squares linear regression was used to develop the functional relationship between ε_{par} and chlorophyll. Model II regression analysis should be used because both the x and y variates are measured with error and the regression parameters are compared (Sokal and Rohlf 1969; Ricker 1973). However, this same relationship has been described extensively in the scientific literature using model I analysis. Consequently, both regression models were used, model I for comparative purposes and model II to show the effect of regression model on parameter estimates.

Photosynthesis methods differ from those reported for the 1972–82 part of Project Quinte (Millard and Johnson 1986; Millard 1986). From 1988 to the present, ^{14}C methodology and a shipboard incubator (described in detail in Fee et al. 1989) have been used to obtain photosynthesis versus light intensity curves (P vs. I). Estimates of the photosynthetic parameters P_m^B (mg C·mg Chl^{-1}·h^{-1}) and α^B (mg C·mg Chl^{-1}·E^{-1}·m^2) were made from these curves using the curve-fitting programs provided by Fee (1990). These parameters along with data for ε_{par}, chlorophyll, mixing depth, and incident solar irradiance were input to the photosynthesis programs of Fee for calculation of daily areal photosynthesis ($\sum P$ = mg C·m^{-2}·d^{-1}) and volume-based rates at optimal light (P_{opt} mg C·m^{-3}·h^{-1}) as well as mean epilimnetic irradiance ($\bar{I}$ = mE·m^{-2}·min^{-1}).

At three stations in GB, photosynthesis was determined in situ at six depths in the water column using the ^{14}C method (described in Sager and Richman 1991). Volume-based rates (mg C·m^{-3}·h^{-1}) were calculated for each depth, areal PP was determined for the incubation period and $\sum P$ was calculated using the light-ratio method (ratio of daily PAR to that for the incubation period). Sampling at the middle and outer bay stations occurred in the summers (June, July, and August) of 1986, 1987, and 1988 with four cruises each summer. At the inner bay station, sampling occurred in summers of 1990, 1991, and 1992 at roughly weekly intervals. ε_{par} and incident PAR were measured using methodology identical to that for BoQ. The sensor for incident PAR was located at the University of Wisconsin-Green Bay campus located on the south shore of Green Bay. Chlorophyll *a* samples were taken from the same depths as ^{14}C incubations, filtered on Whatman GF/F filters, steeped in 90% acetone for 24 h, and analyzed spectrophotometrically (Lorenzen 1967). Values reported here are corrected for phaeopigments.

Phosphorus samples were analyzed according to standard methods (American Public Health Association 1985). The mean summer phosphorus concentration for inner GB was based on four to eight samplings each summer at five stations. Phosphorus concentration ([P]) data prior to 1986 are from Sager and Wiersma (1975), Richman et al. (1984), and Sager et al. (1984). Beginning in 1986, [P] data were from the monitoring program of the Green Bay Metropolitan Sewerage District (Sachs 1992).

$\sum P$ for GB was recalculated using the Fee (1990) programs to compare the effect of controlling chlorophyll and

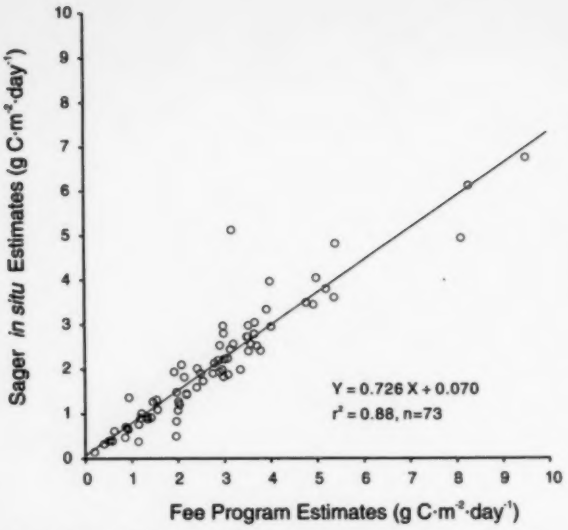

FIG. 3. Daily estimates of integral photosynthesis obtained with the in situ method and extrapolated using the ratio of irradiance received during the incubation period to total irradiance for the day vs. estimates made by reformulating in situ data for input into the Fee programs. Least squares linear regression equation is shown.

background light extinction (ε_w the intercept of the ε_{par} vs. chlorophyll linear regression). Recalculation helped remove variability in estimates of areal PP due to different methods of calculation. Bower et al. (1987) concluded from whole-lake experiments that both in situ and incubator methods gave similar accurate predictions of whole-lake primary production provided in situ data were reformulated to run in the Fee programs as we have done here. To use the Fee programs for GB, the in situ depth profiles of photosynthesis were replotted as P versus I curves using the average irradiance received during the incubation time and ε_{par} to calculate a mean level of irradiance for each exposure depth. A value of 10% was subtracted from incident irradiance to account for reflection. In general, curve fits to the P versus I relationships were good but were based on fewer points than the incubator estimates in BoQ. Surface points showing inhibition were excluded from curve fits for GB because the Fee equations do not account for photoinhibition. BoQ curves rarely showed inhibition because light levels in the incubator were not high enough. Incident irradiance was measured on the day of incubation but continuous daily data were not available for GB. Consequently, cloudless irradiance based on latitude and atmospheric conditions was calculated by the Fee programs and used for the estimates of areal PP for the June 10 – August 31, 1991, period in the control scenarios. Data from cloudy days for in situ experiments were excluded (16 of 89 experiments excluded) from the comparison of the two methods of calculating daily rates of areal photosynthesis because the Fee estimates were based on cloudless irradiance. The light-ratio method originally used to calculate $\sum P$ in GB consistently underestimated $\sum P$ compared to estimates made with the Fee equations and cloudless irradiance as indicated by the slope (<1) and high r^2 in the relationship (Fig. 3).

Background

Both water bodies are separated from their main lake basins by substantial land forms. GB on the northwest corner of Lake Michigan (Fig. 1) is bounded to the east by the Door County Peninsula and a chain of islands, the largest of which is Washington Island. GB is described by Martin (1965) as a submerged hanging valley because its maximum depth (54 m at a point 7 km west of Washington Island) is considerably less than that of the main lake (150–175 m, 30 km to the east of the bay mouth). The mouth of the bay is made up of five passages, all but one deeper than 30 m, for a total cross-sectional area of 0.52 km^2 which permits substantial water exchange with the main lake (Mortimer 1965).

The BoQ on the northeast shore of Lake Ontario is separated from the main lake by Amherst Island and Prince Edward county (Fig. 2). Like GB, the BoQ has glacial origins but the result is a multiple-basin structure with a northeast–southwest alignment that coincides with the direction of late glacial flow and earlier drainage patterns (Sly 1986). Maximum depth of 52 m is located near the mouth of the bay. Shallow sills in the gaps on either side of Amherst Island influence the exchange of water with the main lake (Freeman and Prinsenberg 1986). The western passage or Upper Gap is 13 m deep and the Lower Gap is 24 m. Total cross-sectional area of the mouth of the bay is approximately 0.09 km^2.

Comparison of the surface character of the drainage basins of both bays reveals an important contrast that affects nutrient export from the watershed. In the BoQ, the lack of soils that export large quantities of phosphorus reduces the importance of runoff nutrients to the bay. Additionally, most of the Prince Edward County runoff drains to the southwest yielding little agricultural nutrient input to the BoQ. Hence, spring runoff is not regarded as a major contributor of nutrients in spite of the large relative drainage area (Sly 1986). The highest population density is found along the north shore of the inner Bay, where the total population was estimated at 60 000 in 1982.

The GB watershed is about one-third forested but much of the remaining area, especially in the southern region, is overlain with pink and reddish-brown clay loams, well suited for dairying and agriculture but also highly capable of exporting phosphorus (Bertrand et al. 1976; Harris et al. 1987). Nutrient runoff from rural lands is consequently an important contribution to southern GB especially in spring (Sager and Wiersma 1975). The population of the Fox River watershed was estimated at 680 000, in 1991, 43% of which was found in the lower Fox River sub-basin.

Morphometry

GB has a larger surface area and volume than BoQ (Table 1). The difference in basin volume is one of several factors that contribute to differences in trophic status of the two bays. The depth gradient in GB is quite steep from inner to middle bay, but it quickly levels off in the mid-bay region. For the BoQ, the transition from the shallow inner bay to the area of maximum depth near the mouth of the bay is more gradual. In GB, the inner bay sampling station is located closer to the main tributary input than in the BoQ. In the outer region of GB the main sampling station is very close to the outlet to the lake but in BoQ the station is about 20 km from the upper gap. The drainage area of the

BoQ is smaller than that of GB but its size relative to the bay area (A_d:A_o) is about seven times greater.

The multiple basins of the BoQ contrast with the single basin shape of GB. The inner bay is 35 km long and 4–8 m deep. The middle bay is 13 km long and increases from 6 to 17 m in depth to the south end. The outer bay (Adolphus Reach) is 16 km long and its depth increases from 17 to 52 m. Thermal stratification is weak and unstable in the inner bay but stable in the middle and outer bays although exchange of water with the lake can disrupt stratification. Thermal stratification is typical of most of GB except the shallow, southern region.

Hydrologic Features

Main tributaries account for 94 and 84% of the projected total catchment discharge to the BoQ and GB, respectively. The major tributary of the BoQ, the Trent River, drains 12 600 km^2 or 69% of the total basin area and enters the inner bay at Trenton. The lower Fox River, the major tributary to GB, drains 16 700 km^2 or 41% of the total basin area and enters the head of the bay at the city of Green Bay.

Tributary discharges dominate the water budget of both bays. In BoQ, the nominal flushing rate based solely on tributary input for the whole bay varies from 2.00 to 3.20 times per year but only 0.25 to 1.03 times per summer for the whole bay for the period 1965–1981. Exchanges with Lake Ontario water increase the calculated flushing rates for the whole bay but only affect the middle and outer bay sections (Minns et al. 1986b). Exchanges with Lake Ontario increases the flushing rate for the outer bay from 2.1 to 3.2 times per year based on tributary inputs to 5.4 to 13.8 times per year.

The flushing rate for GB as a whole is much lower at 0.17 times per year based on its volume and mean tributary discharges (Table 1). For the shallow, southern region between the mouth of the Fox River and Long Tail Point and Point Sable; however, the flushing rate ranged from 15.6 to 37.2 times per year for the period 1970–91 based on mean annual flows of the Fox River (P. Sager, unpublished data). In addition, substantial exchange of water between Lake Michigan and the outer bay area causes flushing rates of three to four times per year during the ice-free period for the northern half of the Bay (S.C. Martin, Civil Engineering Department, Youngstown State University, Youngstown, OH). Consequently, the actual annual flushing rate for GB is likely much higher than 0.17.

Phosphorus Loading

Most of the phosphorus load to BoQ and GB is discharged to the inner, eutrophic region of the bays. The phosphorus load actually discharged at the mouth of the lower Fox River to GB is generally less than the total load delivered to the river in the basin because of retention caused by locks and hydroelectric dams along the river. The difference is variable depending on flow rate, which varies seasonally and annually with precipitation.

Reduction of point-source phosphorus loadings was initiated in both basins in the mid-1970s following the recommendation of the International Joint Commission and the signing of the Great Lakes Water Quality Agreement in 1972. The reduction in point-source loads to the two bays was substantial and very similar, 90 and 84% for BoQ and GB, respectively, although the GB data are based on a comparison of just one pre- and one post-control year (Table 2). The small reduction in total load indicates the magnitude of nonpoint phosphorus sources in both basins.

TABLE 1. Comparative morphometry and hydrology of the Bay of Quinte and Green Bay.

Feature	Bay of Quinte	Green Bay
Surface area (km^2)	257	4520
Drainage basin (km^2)	18 200	40 500
A_d:A_o[a]	70	9.5
Length (km)	64	193
Mean width (km)	4	22
Mean depth (m)	9.7	17
Inner bay[b]	5.0	3.5
Middle bay	12.0	27.0
Outer bay	33.0	28.0
Volume (km^3)	2.5	67
Total tributary flow (m^3·s^{-1})	195	336
Flushing rate (yr^{-1})	2.0–3.2	0.17

[a]A_d:A_o = ratio of drainage basin to bay surface area.
[b]Depths for the regions of each bay are the depths at sampling stations.

The two bays differ in several important aspects of their total P loading, most notably in the importance of tributary loading. The river load of phosphorus to GB is mostly in the form of algae exported from Lake Winnebago, especially from late spring through fall but the effectiveness of this load in enriching the bay depends on remineralization and recycling rates within the bay. Most point sources in the lower Fox River drainage basin discharge to the Fox River with the exception of the Green Bay Metropolitan Sewerage District, which discharges its effluent at the mouth of the Fox River. The river load of P to BoQ has less net enrichment effect than in GB because it has low concentration compared with the Fox River and point sources in the BoQ and has a concentration similar to the receiving BoQ waters. These relatively low river concentrations in BoQ occur because most point sources discharge directly to BoQ and not via tributaries as in GB. Additionally, river inputs of P to BoQ are highest in the spring and fall when flows are high; however, these high flows flush most of the P load through the bay (Johnson and Owen 1971). In contrast, point-source loading has the biggest impact on water quality in BoQ during the summer because these inputs are high concentration relative to the bay and have negligible flow to help flush the bay. As a result, the decline in summer river flow allows concentrations to increase in the inner bay and causes the high levels of phytoplankton biomass and photosynthesis that occur in the inner bay during summer (Millard and Johnson 1986).

Minns et al. (1986b) suggest that control of the P budget in inner BoQ shifted from external to internal loading between pre- and post-treatment periods. For GB, nonpoint sources now contribute the majority of the P load. Internal loading in the Fox River and inner bay is likely important as well but has not been documented.

Trophic Status

Response to P controls is discussed here primarily for the eutrophic portions of the two bays. The change in mean summer [P] following point-source load reduction in BoQ is

TABLE 2. Comparative phosphorus loading ($kg \cdot d^{-1}$), and total phosphorus and chlorophyll ($mg \cdot m^{-3}$) concentrations (June, July, and August means) for the inner Bay of Quinte and Green Bay.

	Bay of Quinte			Green Bay		
Variable	Pre-P control	Post-P control	% reduction	Pre-P control	Post-P control	% reduction
Total external P[a]	882[b]	842[b]	5	2795[c]	1918[c]	31
Point source P	157[d]	16[e]	90	1014	164	84
Total P	82±30[f]	46±18	44	206±29[g]	147±15	29
Chlorophyll *a*	29±18	17±12	41	98±28[h]	61±25	38
Secchi disc (m)	1.1	1.3	ns[i]	0.5	0.5	0

[a]Total = river + atmospheric + point source loads.

[b]Mean annual loading 1972–77 from Minns et al. (1986b). Pre-P control = 1972–77; post-P control = 1978–81.

[c]Pre-control, external, and point-source P loadings are from 1970 (Sager and Wiersma, 1975). Post-control loadings are from 1990 (Wisconsin Department of Natural Resources 1993).

[d]Summer (May–Oct.) loading (1973–77) from Bay of Quinte Remedial Action Plan monitoring report 3. Ontario Ministry of the Environment and Energy, Kingston, Ontario.

[e]Summer (May–Oct.) loading 1991, from Bay of Quinte Remedial Action Plan monitoring report 3.

[f]Data for total P and chlorophyll are June–Aug. means for location I in the inner bay. Pre-control is 1973–77 (n = 51) for chlorophyll and 1972–77 (n = 78) for total P. Post control is 1978–91 for both variables (n = 116).

[g]P concentrations are June–Aug. means. Pre-P control = 1970–77 (n = 197); no data for 1974–75. Post-P control = 1982–91 (n = 411) no data for 1983. The mean is based on sampling at five locations, all very close to location I on the GB map.

[h]Chlorophyll concentrations are June–Aug. means for location I. Pre-control is 1976–77 (n = 15). Post-control = 1982–91 (n = 82); no data for 1983.

[i]ns = not significant.

documented for the middle and outer regions of the bay but the greatest change has occurred in the inner region (Robinson 1986).

The change in [P] following point-source load reductions has been greater for BoQ (Table 2). Mean summer [P] in the inner BoQ declined 44% following P control. Summer means were calculated for June to August in BoQ to be consistent with those of GB. In BoQ (but not GB) data were available for May to early October and summer means would be higher if calculated for July to September, the period of highest chlorophyll and phosphorus concentrations. For example, pre-control concentrations of phosphorus and chlorophyll would have been 97.0 and 42.0 $mg \cdot m^{-3}$, respectively, for July to September. The relative decline in the post-control period would have been the same for phosphorus and slightly higher (47%) for chlorophyll. [P] declined 26%, from 48 to 36 $mg \cdot m^{-3}$ in the middle BoQ following controls. Concentrations showed no change in the outer bay where they averaged only 18–20 $mg \cdot m^{-3}$ for both periods. Reduction in [P] for inner GB was substantial but not as great as in the BoQ because pre-control values of 206 $mg \cdot m^{-3}$ were much higher. [P] for the middle and outer regions of GB are not available for the pre-control period. Limited data for the post-control period for these two regions in 1986 indicate mean [P] of 17.5 and 9.0 $mg \cdot m^{-3}$ for the middle and outer parts of the bay, respectively.

The decline in mean summer chlorophyll *a* was proportional to [P] in both bays. Reduction was greater in the BoQ but pre-control values were only 33% of those in GB. Summer mean chlorophyll for the BoQ in 1991 was 25.3 $mg \cdot m^{-3}$ (range 6.2–39.2, n = 7) compared with a mean for inner GB during 1991 of 40.6 $mg \cdot m^{-3}$ (range 13.1–69.2, n = 20). The difference in chlorophyll concentrations between the two bays may be slightly higher because GB chlorophyll data are corrected for phaeopigments and BoQ data are not. The phaeopigment correction based on linear regression would lower BoQ values by about 10–15% in the 25–50 $mg \cdot m^{-3}$ concentration range (inner bay 1977–91, uncorrected = 0.93 (corrected) − 1.88, r^2 = 0.98, n = 241).

Summer levels of chlorophyll show substantial temporal variability in both bays but may be more pronounced in GB. Composition of the phytoplankton community in both bays probably contributes to temporal variability. For example, chlorophyll variability is associated with development and decline of cyanobacteria blooms which have exceeded chlorophyll *a* concentrations of 100 $mg \cdot m^{-3}$ in GB in pre-control years. Cyanobacteria constitute 76% of the phytoplankton community in inner GB (Rhew 1992) but their contribution is more variable in BoQ. The large filamentous diatom *Melosira* dominated the phytoplankton community in BoQ both before and after P controls (Nicholls et al. 1986). Species of this genus require constant vertical mixing to remain in suspension owing to their rapid sinking rates (Lund 1954), and, consequently, chlorophyll levels may vary owing to sedimentation and resuspension of dense populations.

Mean Secchi disc transparency changed little in both bays following P controls (Table 2) because Secchi disc measurement is insensitive to changes in transparency when levels of chlorophyll are high (Megard et al. 1980). Vertical light

TABLE 3. Results of model I least-squares regressions between ε_{par} and chlorophyll *a* for the main regions of Green Bay and the Bay of Quinte. Regression parameters in parentheses were obtained with model II regression.

Location	ε_w[a]	ε_s[b]	r^2	n	p
Green Bay[c]					
Inner	1.69±0.15 (1.33)	0.026±0.004 (0.039)	0.44	55	<0.01
Middle	0.43±0.036 (0.40)	0.024±0.006 (0.030)	0.63	11	0.03
Outer	0.31±0.019 (0.30)	0.018±0.005 (0.022)	0.63	11	0.04
Bay of Quinte[d]					
Inner	0.91±0.022 (0.81)	0.024±0.001 (0.027)	0.77	385	<0.01
Middle	0.73±0.021 (0.67)	0.020±0.001 (0.023)	0.75	272	<0.01
Outer	0.41±0.012 (0.33)	0.024±0.001 (0.032)	0.55	411	<0.01

[a]ε_w = intercept in the regression of ε_{par} vs. chlorophyll *a*. Represents nonchlorophyll *a* background extinction.

[b]ε_s = slope of the regression line. Increment in ε_{par} per unit increase in chlorophyll *a* ($mg^{-1} \cdot m^{-2}$).

[c]Data for inner GB are June, July, and August 1990–92; middle and outer GB are June, July, and August 1986–88.

[d]Inner Bay analysis is for locations I and N, middle bay location M and P, and outer bay for GL, O, LE, May–October 1977-91. Analysis is for same station groupings representing the three regions of the bay as in Millard (1986).

extinction improved 23% for the summer months in the inner BoQ following P control. ε_{par} values for inner GB were extremely high; on 6 of 11 sampling dates in 1991 values exceeded 3.0 m^{-1} and on one occasion ε_{par} was over 4.0 m^{-1}. These extreme values are characteristic of shallow highly eutrophic areas where both chlorophyll and suspended sediments can be high (Ganf 1974). Cootes Paradise, Hamilton Harbour, is another Great Lakes AOC where extreme values of ε_{par} can be found owing to these same factors and causes very shallow euphotic zones (Z_{eu}) (E.S. Millard and D.S. Painter, unpublished data). On only a few occasions prior to P control did ε_{par} exceed 3.0 m^{-1} in the inner BoQ (Millard and Johnson 1986).

Trophic Gradients

The gradient in [P] from inner to outer GB and BoQ is one of the main determinants of the gradient in algal biomass in both systems. Based on chlorophyll concentrations and ε_{par}, GB is more eutrophic in the inner bay and has a steeper gradient from inner to outer bay than the BoQ (Table 3). Trophic conditions at the middle and outer regions of GB are influenced markedly by the frequency of water exchange with meso-oligotrophic Lake Michigan. Similar exchanges with Lake Ontario influence the trophic status of the water mass in the outer BoQ (Freeman and Prinsenberg 1986; Minns et al. 1986b). However, chlorophyll, phosphorus and ε_{par} are still higher in the outer BoQ than in the nearby Kingston basin at the east end of Lake Ontario (O.E. Johannsson and E.S. Millard, unpublished data, Bioindex Project, Department of Fisheries and Oceans, Burlington, ON).

The shallow depth and high loadings of nutrients and suspended solids from the Fox River cause the extreme eutrophic conditions at the head of GB. Conditions are similar in BoQ but loading of suspended solids from the Trent River are not as high as in GB. Total seston dry weight in BoQ varied from 3.6 to 23.0 $mg \cdot L^{-1}$ from spring to fall (1991) with a mean of 10.1 $mg \cdot L^{-1}$. The mean ash content of the seston in these measurements is 42%, indicating that suspended solids are only about half of the seston measurements at most. Seston measurements in GB have a range of 8 to 67 $mg \cdot L^{-1}$ with a mean of 28 $mg \cdot L^{-1}$.

Underwater Light Climate

The amount of light in the mixed layer (Z_m) is a key factor influencing the depth profile of PP. Background light extinction (ε_w), due to nonchlorophyll factors such as dissolved substances and suspended nonalgal particulates, competes with photosynthetic pigments for available PAR and limits the proportion of the phytoplankton community that can contribute to water-column photosynthesis. The intercept of an ε_{par} versus chlorophyll *a* plot (Fig. 4) has been used extensively to represent ε_w and is high in both GB and BoQ compared with other water bodies (Robarts 1979; Field and Effler 1983). Use of model II regression had the most effect on regression parameters where r^2 was low because model II slope = model I slope/r. The gradient in ε_w was still evident in both bays using model II analysis but ε_w for inner GB was lowered by about 21% compared with the model I estimate. ε_w in BoQ was lowered throughout the bay using model II but the gradient was still evident. High and variable loads of suspended sediment from the Fox River are the cause of extreme values for ε_w in GB and are the likely cause of the lower r^2 in the ε_{par} versus chlorophyll regression for GB. Sediment load from the Trent River contributes to

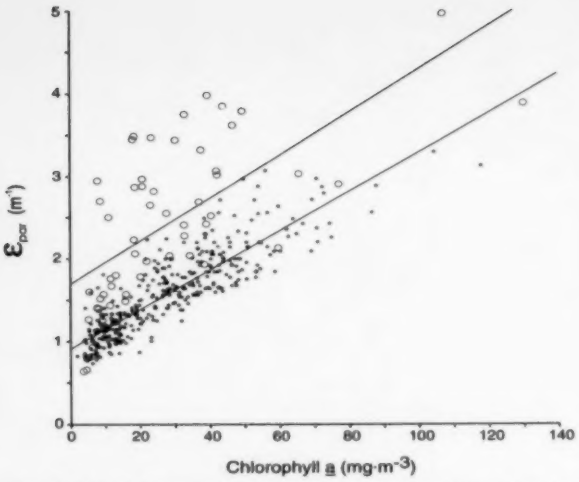

FIG. 4. Model I regressions of ε_{par} versus chlorophyll *a* for the inner regions of both Green Bay (upper line, open circles) and the Bay of Quinte (lower line, stars). See Table 3 for regression parameters.

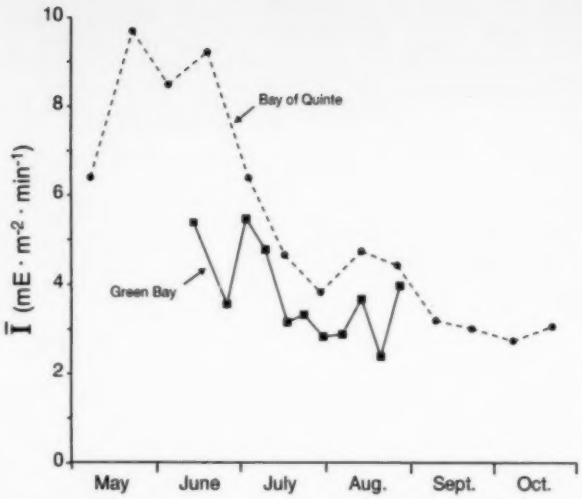

FIG. 5. Seasonal trends in $\bar{I}$, the mean epilimnetic irradiance, for inner Green Bay and the Bay of Quinte. Values were calculated using theoretical cloudless irradiance.

ε_w in BoQ but may only be important in the spring at peak flow when phytoplankton growth is also controlled by temperature as well as light and nutrients. Dissolved organic matter from adjacent marshes and resuspended sediments in the shallow, well-mixed inner bay probably contribute most to the high average ε_w in BoQ.

High background light extinction (ε_w) limits the lower extent of photosynthesis versus depth profiles. When ε_{par} is due primarily to algal pigments a theoretical maximum for the euphotic zone content of chlorophyll (ΣChl) and an upper limit to areal photosynthesis can be calculated (Bannister 1974; Megard et al. 1979). Talling (1965, 1971) showed that in most lakes ΣChl can be defined by a constant of 3.7 divided by the self-shading coefficient (ε_s = mg^{-1}·m^{-2}), the slope of the ε_{par} versus chlorophyll regression. Millard (1986) and others (Jewson 1976; Jones 1977) have found that a value of 3.9 is more appropriate in eutrophic sites. Theoretically, the maximum ΣChl in GB would be defined as 3.9/0.026 or 150 mg·m^{-2} of chlorophyll *a* and marginally higher in the BoQ (163 mg·m^{-2}) because of a slightly lower value of ε_s (0.024). The estimate of ΣChl would be considerably lower for GB (100 mg·m^{-2}) using the estimate of ε_s from the model II regression. High ε_w in GB increases ε_{par}, shortens Z_{eu} and lowers ΣChl comparatively more than if ε_{par} increases due to an increase in chlorophyll. Background light extinction lowers chlorophyll that could exist in the euphotic zone ($\varepsilon_w/\varepsilon_s$) and contribute to areal photosynthesis. If the high values for ε_w of 1.69 and 0.91 m^{-1} for GB and BoQ were zero, ΣChl would be an additional 70 and 38 mg·m^{-2} higher in each bay, respectively.

There is a distinct gradient in ε_w in both bays from the inner to outer regions (Table 3). The self-shading coefficient (ε_s) is similar in both bays, does not show the same gradient as ε_w, and is high in these bays compared with other lakes if model I regression analysis is used (Field and Effler 1983; Reynolds 1984). Model II analysis increased the variability in the estimates of ε_s. Values were much higher in inner GB and outer BoQ, indicating opposite gradients not evident using model I analysis. Similar to the effect of ε_w, self-shading also lowers ΣChl and is complete when ε_{par} is due only to chlorophyll and is equal to 3.9/ε_s (Talling 1965). ΣChl is at a maximum under complete self-shading because increases in chlorophyll per unit volume do not increase ΣChl because of the negative effect on Z_{eu}.

Physical factors such as mixing depth (Z_m) and light extinction (ε_{par}) are important in determining the light regime for vertically mixed phytoplankton communities (Table 4). The photosynthesis programs of Fee (1990) compute $\bar{I}$ from the interaction of incident solar irradiance, ε_{par}, and Z_m. $\bar{I}$ was calculated using theoretical cloudless irradiance because continuous empirical solar irradiance data were unavailable for GB. $\bar{I}$ calculated with cloudless irradiance is best for elucidating trends in the relative influence of Z_m and ε_{par} on $\bar{I}$ because variability due to cloudy weather is removed. In spite of shallower depth, the mean summer $\bar{I}$ for inner GB was only 60% of the inner BoQ mean because of much higher ε_{par}. The difference in $\bar{I}$ was even more pronounced early in the season (Fig. 5) because of much lower values of ε_{par} in BoQ compared with GB (Table 4).

Although Z_m is constant in the fully mixed, shallow, inner bays, the middle and outer regions of both bays have a variable Z_m because of seasonal trends in thermal stratification. Seasonal changes in Z_m were considered to be a controlling factor for phytoplankton growth in the outer BoQ because deeper Z_m reduces $\bar{I}$ causing light limitation of growth (Millard 1986). A gradient of increasing $\bar{I}$ from inner to outer bay was expected in both bays owing to a gradient of increasing transparency. However, the gradient in $\bar{I}$ was more pronounced in GB because ε_{par} decreased more in the outer bay compared with BoQ. ε_{par} decreased towards the lake in BoQ, but the mixed layer was deeper under stratified conditions and $\bar{I}$ was lower as a result. $\bar{I}$ in the outer BoQ declines to levels considered limiting to phytoplankton growth (1–3 mE·m^{-2}·min^{-1}; Hecky and Guildford 1984) under conditions of full mixing during the spring and fall and would be even less under actual levels of solar irradiance.

TABLE 4. Comparative light climate and photosynthetic rates for the regions of the Bay of Quinte and inner Green Bay (1991) and middle and outer Green Bay (1988). Means (±1 SD) are for June, July, and August except ε_w and ε_{par}, which are derived from regressions.

Variable	Green Bay			Bay of Quinte		
	Inner	Middle	Outer	Inner	Middle	Outer
Depth (m)	3.5	27.0	28.0	5.0	11.0	31.0
Epilimnion depth (Z_m; m)	3.5	11.0±0.5	10.5±0.6	5.0	6.6±3.6	14.3±4.4
Euphotic zone depth (Z_{eu}; m)	1.5±0.4	8.3±1.4	13.7±1.1	3.4±1.0	5.2±1.6	10.4±1.7
Light extinction (ε_{par}; m^{-1})	3.18±0.74	0.57±.11	0.34±0.03	1.46±0.42	0.96±0.32	0.45±0.07
Background extinction (ε_w; m^{-1})	1.69	0.43	0.31	0.91	0.73	0.41
Mean epilimnetic irradiance						
$\bar{I}$ ($mE \cdot m^{-2} \cdot min^{-1}$)[a]	3.77±1.03	6.65±1.3	10.60±1.5	5.96±2.1	9.40±6.9	7.10±3.6
$\bar{I}$[b]	—	—	—	4.59±2.2	7.67±6.5	5.81±2.3
Photosynthesis						
P_{opt} ($mg\ C \cdot m^{-3} \cdot h^{-1}$)[c]	507±179	13.5±9.4	7.1±5.9	147±91	98.6±93.5	23.6±18.1
$\sum P$ ($mg\ C \cdot m^{-2} \cdot d^{-1}$)	3732±116	700±369	438±316	2411±112	2436±140	1322±849

[a]Calculated using theoretical cloudless irradiance computed by the programs of Fee (1990).
[b]Calculated using empirical solar irradiance. Data not available for GB.
[c]Photosynthesis at optimal light conditions.

Photosynthesis

Both P_{opt} and $\sum P$ are much higher for inner GB than for inner BoQ (Table 4). P_{opt} in BoQ prior to P controls approached the high rates measured in inner GB in 1991 but rates have declined dramatically in recent years compared with pre-P-control rates (Millard and Johnson 1986). In spite of large differences between the inner bays of both GB and BoQ in P_{opt}, chlorophyll levels did not differ proportionately. This suggests that either chlorophyll concentrations were underestimated for GB or chlorophyll specific rates of photosynthesis are much higher in GB. Higher rates per unit chlorophyll are likely part of the explanation given the warm temperatures, shallow, well-mixed water column, and the high nutrient levels. On the other hand, the technique used for chlorophyll analysis in GB is the same method that was found to underestimate chlorophyll at peak biomass in the BoQ (see Millard and Johnson (1986) for details). Given the high levels of algal biomass and dominance of blue-green algae, underestimates of chlorophyll for inner GB cannot be ruled out.

P_{opt} in inner GB was substantially higher (3.4 times) than for inner BoQ, but mean summer $\sum P$ was only 1.5 times higher. This is consistent with a shift from phosphorus to light as the controlling factor for $\sum P$ along the trophic gradient in GB as noted by Sager et al. (1984). The $\sum P$ in GB was limited by high values of ε_{par} due to light absorption by suspended particulate matter that reduced the euphotic zone chlorophyll content ($\sum$Chl) and areal photosynthesis. When chlorophyll, and not abiotic suspended solids, is dominant in absorption of ε_{par}, the negative effect on $\sum P$ of decreases in Z_{eu} is offset by the positive effect that higher chlorophyll has on P_{opt} and $\sum P$ is maximized. Competition for PAR by non-algal sources decreases areal PP because Z_{eu} is shortened but there is no corresponding increase in volume-based rates of photosynthesis as there is when ε_{par} increases due to chlorophyll. This effect was more noticeable in the inner BoQ prior to P control when the underwater light climate was considered to be limiting to net production at peak standing crop (Millard 1986). The depth profiles of photosynthesis integrated over time by the photosynthesis programs of Fee (1990) show the high rates per unit volume in inner GB compared with BoQ and the truncated nature of the profile due to rapid light extinction (Fig. 6). This is much less pronounced for the inner BoQ and for other regions of both bays. The depth profile of photosynthesis for the outer BoQ is very similar to that for middle GB as pointed out for other trophic indices.

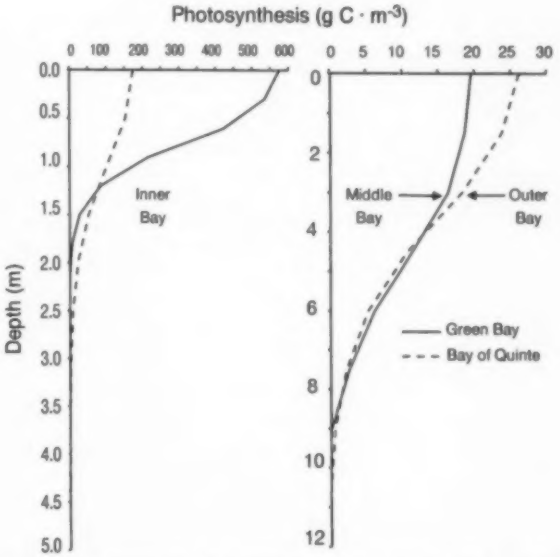

FIG. 6. Depth profiles of photosynthesis integrated from June 10 to August 31, 1991, for inner and outer Bay of Quinte and inner Green Bay and for the same period in 1988 for middle Green Bay.

TABLE 5. Modelled effect of changes in chlorophyll and background light extinction (ε_w) on areal photosynthesis ($\sum P$) (June 10 – August 31, 1991) and mean epilimnetic irradiance ($\bar{I}$; $mE \cdot m^{-2} \cdot min^{-1}$). Baseline background light extinction in the 0% reduction scenario was the intercept from the ε_{par} vs. chlorophyll regression for both bays (see Table 3).

	Chlorophyll		ε_w	
% reduction	$\sum P$ (g C·m^{-2})	$\bar{I}$	$\sum P$ (g C·m^{-2})	$\bar{I}$
Green Bay				
0	583	4.54	473	3.77
25	476	4.93	556	4.44
50	349	5.40	670	5.37
75	193	5.97	857	6.91
Bay of Quinte				
0	201	5.02	215	5.53
20 (ε_w Middle Bay)[a]			244	6.40
25	170	5.58		
50	130	6.30		
75	77	7.26		

[a]Background extinction ε_w lowered from 0.91 m^{-1} to the middle bay value of 0.73 m^{-1}.

Remedial Action Scenarios and Their Effect on Integral Photosynthesis

A primary goal in the RAPs for both bays is to lower phosphorus loadings and thus chlorophyll levels. The goal in GB is to reduce present phosphorus loadings to 50% (Wisconsin Department of Natural Resources 1993) and in BoQ to reduce in-bay [P] to 30 mg·m^{-3} (Stride et al. 1992). In GB this action would result in about a 50% reduction in chlorophyll concentrations and in the BoQ, [P] of 30 mg·m^{-3} would result in mean chlorophyll levels of only 16 mg·m^{-3} compared with a summer mean of about 25 mg·m^{-3} for 1991. In addition, a further goal of the GB RAP is to lower suspended solids loadings by 50%, an action that should lower ε_w in the inner bay.

We attempted to predict the effects of these remedial actions on water column photosynthesis using the Fee photosynthesis programs. The data subsets required as input to calculate $\sum P$ (transparency, chlorophyll, photosynthetic parameters, and mixing depth) can be manipulated to predict the effect that changes in these variables would have while other conditions are held constant. The two variables of interest from a management perspective were background light extinction and chlorophyll concentration. Our hypothesis for ε_w scenarios was clear: lowering ε_w would increase $\sum P$ because of the increase in Z_{eu}, but the extent of the increase relative to changes in ε_w was unknown. The effect of reducing chlorophyll levels was more complex because reduced levels would increase $\sum P$ because of improved transparency but the increase would be partially offset by a proportional decline in volume-based rates throughout the water column. Predicting the outcome of the opposing effects of the two variables would not be possible without a numerical model.

We ran various scenarios of control that encompassed a reduction scenario (50%) consistent with RAP goals (Table 5). There was no stated goal in the BoQ RAP related to background light extinction however, the distinct gradient in ε_w from inner to outer bay invited the question: how much would integral photosynthesis increase in the inner bay if ε_w were as low as the middle bay? This was the only scenario related to ε_w that was run for BoQ.

The value of background light extinction from model I regression was used for the control scenarios because the relative effects of reducing ε_w was the primary focus rather than the absolute value of the parameter itself. The background light extinction was manipulated as follows for the control scenarios: measured ε_{par} for each date was reduced by the percentage for the control scenario times ε_w for inner GB (1.69 m^{-1}). For example, if measured ε_{par} was 2.5 m^{-1}, a 25% reduction in ε_w would result in ε_{par} of 2.08·m^{-1} (2.5 − 0.25 × 1.69 m^{-1}). For the BoQ ε_w scenario, measured ε_{par} was reduced by the difference in ε_w for the inner and middle bays (0.91–0.73 m^{-1} = 0.18 m^{-1}). For the chlorophyll scenarios, concentrations were reduced proportionately and the effect on light extinction was predicted using the regression equations relating ε_{par} to chlorophyll (Table 3). As a result, $\sum P$ differs at the zero reduction level between the chlorophyll and ε_w scenarios because ε_w scenarios use measured ε_{par} for each sampling date but chlorophyll scenarios use predicted ε_{par} that is different because of variability in the predictive equation. The difference is more notable for GB (compare 583 with 473 g C·m^{-2}) where the ε_{par} versus chlorophyll relationship was more variable (r^2 = 0.44) compared with BoQ (r^2 = 0.77). Variability in the contribution of suspended solids to ε_{par} in GB is likely the cause but underestimation of chlorophyll may also be a factor. However, this error was considered acceptable since our primary goal was to demonstrate relative changes within control scenarios. The agreement for $\sum P$ at zero reduction for both ε_w and chlorophyll scenarios in BoQ was remarkably close indicating the regression equation for BoQ is accurate at predicting ε_{par}.

As expected, lowering background light extinction (ε_w) in GB had a very pronounced positive effect on areal photosynthesis ($\sum P$) (Table 5). At a 50% reduction in ε_w, $\sum P$ increased 42% with a corresponding increase in $\bar{I}$. Reducing ε_w in the inner BoQ had a fairly limited effect since the absolute change in ε_{par} was only 0.18 m^{-1} compared with a reduction of 0.85 m^{-1} for ε_{par} in the 50% scenario for GB. Reducing chlorophyll had an equal but opposite effect on photosynthesis. At a 50% reduction in chlorophyll for GB, $\sum P$ declined 40% but $\bar{I}$ increased only 19%. Clearly, the negative effect of reducing photosynthetic rates per unit volume had a greater impact on areal photosynthesis than the small increases in Z_{eu} that occurred. For example, at a chlorophyll concentration of 40 mg·m^{-3}, ε_{par} predicted from the regression equation is 2.73 m^{-1} (Z_{eu} = 1.7 m) but a 50% reduction in chlorophyll would reduce ε_{par} to 2.21 m^{-1} (Z_{eu} = 2.1 m) for an increase in Z_{eu} of only 0.4 m. Other researchers have pointed out the importance of P_{opt} in maintaining high integral rates of photosynthesis (Talling,1965; Sager et al. 1984).

These data manipulations were used to indicate the potential effects of proposed remedial actions on photosynthesis. Their effect was instantaneous in the programs but would undoubtedly be part of a complex response in the ecosystem that would be integrated over a longer time period. For example, as ε_w declines light conditions in the water column would improve and could lead to an increase in phytoplankton biomass as light limiting effects of high ε_w are

alleviated, thus producing a negative feedback through the influence of the increased chlorophyll on ε_{par}.

The high phytoplankton biomass of both inner bays is dominated by large-celled species that have shown most of the decline under reduced P loadings (Nicholls et al. 1986; Richman and Sager 1990). These larger forms usually have considerably lower rates of photosynthesis per unit biomass than smaller cells (Pollingher and Berman 1982; Pick and Caron 1987). A significant reduction in chlorophyll may not be followed by a corresponding reduction in photosynthesis since the contributions of small versus large size fractions is disproportionate to biomass. Thus $\sum P$ could potentially be maintained at similar levels despite reductions in chlorophyll, as it is during the midsummer P-limited period in Lake Ontario (E.S. Millard, unpublished data).

Management Implications

We have tried to compare the lower trophic level response with changes in P loads and underwater light climate for two economically important and culturally eutrophic AOCs on the Great Lakes. There is an obvious need to integrate results from research and monitoring programs in AOCs because cultural eutrophication is a problem common to many of them. Communication between studies and integration of results can only benefit our understanding of rehabilitative mechanisms. Our goal was to point out important similarities and differences in light, nutrient, and physical factors that control phytoplankton growth in these environments. Recovery of submerged macrophytes in these bays will be contingent on an improved underwater light climate. Understanding how various factors such as depth, suspended sediment, chlorophyll, and self-shading characteristics of the phytoplankton crops influence this important ecological parameter may help in this recovery. An understanding of the relative contributions that various particle types (sediment vs. phytoplankton) make to ε_{par} will help in making cost-effective management decisions to improve light conditions for future macrophyte development.

It was possible to predict the relative response of one important ecosystem property, phytoplankton photosynthesis, to proposed remedial actions. Numerical models such as those of Fee (1990), where a number of factors can be manipulated, is useful in understanding the potential response to controlling variables.

Our understanding of the relationship between changes in P loading and standing crop of algae is reasonably good, but knowledge is lacking on how degraded ecosystems move to rehabilitated states that are likely to differ from their "original condition." Rehabilitation studies are still in their infancy in the Great Lakes ecosystem because protocols for nutrient management have been in place only 15 yr. This may be a long time frame for scientific studies but may be inadequate for understanding ecosystem responses to management actions against the backdrop of natural variability. Researchers in the GB and BoQ studies must be encouraged to maintain monitoring programs so that information from these long-term studies can be of benefit in other AOCs where long-term studies are lacking. As Schindler (1987) points out, ecosystem monitoring must be encouraged and developed as a science in its own right if we are to learn from nutrient management actions. Standardization of methods through consultation with other agencies and countries at the outset of monitoring would go a long way to ensuring that long-term data sets are comparable.

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Mysis relicta: Assessment of Metalimnetic Feeding and Implications for Competition with Fish in Lakes Ontario and Michigan

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Mysis relicta and planktivorous fish in Lakes Ontario and Michigan both feed on crustacean zooplankton in the metalimnion. Are these zooplankton sufficient to meet the energy requirements of mysids? Could mysids remove a significant proportion of zooplankton production? Are the energy requirements in the two lakes similar? Comparisons in Lake Ontario of zooplankton consumption based on clearance rates, with energy requirements based on bioenergetic modelling, revealed that individual mysids, particularly larger ones, required additional energy sources. The denser mysid populations beyond 100 m depth in Lake Ontario could exert high mortality rates on metalimnetic zooplankton, remove a significant proportion of daily zooplankton production, and consequently, potentially compete with planktivorous fish. At depths <100 m, the mysid population was smaller and could remove only 6–19% of zooplankton production per day in summer when competition with planktivorous fish would be maximal. Generation time is shorter in Lake Michigan because winter growth rates remain high. Consequently, less energy is required to complete a generation in Lake Michigan than in Lake Ontario.

Mysis relicta et les poissons planctivores des lacs Ontario et Michigan s'alimentent tous deux de crustacés trouvés dans le zooplancton du métalimnion. Y-a-t-il suffisamment de ce zooplancton pour répondre aux besoins énergétiques des mysidés? Ceux-ci peuvent-ils prélever à leur profit une proportion importante de la production zooplanctonique? Les besoins en énergie sont-ils les mêmes dans les deux lacs? Dans le lac Ontario, le rapprochement entre la consommation de zooplancton établie sur les taux d'élimination, et les besoins énergétiques établis d'après une modélisation bioénergétique, a révélé que les mysidés individuels, notamment les plus gros, doivent trouver des sources additionnelles d'énergie. Les populations plus denses de mysidés au-delà de 100 m de profondeur, dans le lac Ontario, pourraient être à l'origine d'une mortalité élevée du zooplancton au niveau du métalimnion, prélever une partie importante de la production quotidienne zooplanctonique et, par conséquent, elles pourraient éventuellement concurrencer le poisson planctivore. À des profondeurs inférieures à 100 m, la population de mysidés était moindre et ne pouvait prélever que seulement 6–19% de la production zooplanctonique par jour durant l'été, alors que la concurrence avec les poissons planctivores serait la plus intense. La durée de vie des générations est plus courte dans le lac Michigan parce que la croissance hivernale reste élevée. Par conséquent, il faut moins d'énergie pour compléter une génération dans le lac Michigan que dans le lac Ontario.

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Mysis relicta, the opossum shrimp, is common in freshwater lakes throughout the northern hemisphere, reaching abundances of over 300 individuals·m^{-2} and a biomass of over 7 g wet wt.·m^{-2} in both Lakes Michigan and Ontario (Grossnickle and Morgan 1979; Sell 1982; Johannsson 1992). *Mysis* spends the day on or close to the bottom of lakes and migrates up to the metalimnion at night (Beeton and Bowers 1982). The ascent is controlled by light levels (Teraguchi et al. 1975; Rudstam et al. 1989) and limited by temperatures above 16–17°C (Beeton and Bowers 1982). An omnivore, *Mysis* feeds on zooplankton, benthos, phytoplankton, and detritus (Grossnickle 1982). It is an important prey for planktivorous (alewife (*Alosa pseudoharengus*), smelt (*Osmerus mordax*), sculpins (*Cottus* spp.), and bloater (*Coregonus hoyi*)) and young piscivorous (lake trout (*Salvelinus namaycush*)) fish (Stewart and Binkowski 1986; Lantry 1991; Mills et al. 1992; Urban and Brandt 1993), and possibly a major competitor of these same fish species for zooplankton. The interactions between mysids, fish, and zooplankton are, therefore, complex (an example of intraguild predation; Polis and Holt 1992) and the result of mysid introductions in lakes have been dramatic and largely unexpected. In many cases, zooplankton populations, especially larger cladocerans, were severely depleted as a result

of mysid predation, and growth and survival of both planktivorous salmonids and young piscivores decreased (Goldman et al. 1979; Lasenby et al. 1986; Koksvik et al. 1991; Martinez and Bergersen 1991). Long-term and comparative studies show that the effects of mysids persist once they have become established (Langeland et al. 1991).

In this paper we evaluate the potential for food competition between mysids and surface-feeding planktivorous fish in Lakes Ontario and Michigan. To investigate whether or not individual mysids can obtain their caloric requirements by feeding solely on metalimnetic zooplankton at night, we estimated the caloric demand of individual mysids in both lakes with a bioenergetics model, and then determined the fraction of this demand that could be met by consumption of crustacean zooplankton given prey-specific clearance rates (from in situ experiments by Bowers and Vanderploeg 1982 and Nero and Sprules 1986), and from zooplankton densities. We then estimated zooplankton consumption by the whole mysid population and compared this with the production of zooplankton in the upper part of the water column. The higher the fraction of zooplankton production that is consumed by mysids the greater the potential competition for food between mysids and planktivorous fish. The analysis is more detailed for Lake Ontario than Lake Michigan simply because more is known about both zooplankton production and mysid abundance and growth in Lake Ontario.

Methods

Sufficient information on zooplankton distributions and production and on mysid abundance and life history was available from Lake Ontario for 1990 to investigate the potential demand of mysids on available zooplankton resources in the surface waters. This information comes from a weekly biomonitoring program (Long Term Biomonitoring (Bioindex) Program, Department of Fisheries and Oceans, Burlington, ON) at a midlake station 28 km south of Cobourg, ON (station 41, 130 m depth; Johannsson et al. 1985; Johannsson 1992) and from whole-lake mysid surveys conducted that year as part of the Lake Ontario Trophic Transfer Study (Johannsson, unpublished data). For Lake Michigan, mysid density data from 1985–89 were taken from Lehman et al. (1990), and mysid life history and mortality rates from Carpenter et al. (1974), Morgan (1976; cited in Sell 1982), and Morgan and Beeton (1978); metalimnetic zooplankton data were not available for Lake Michigan.

For the purposes of this study, the mysid population was assumed to occupy and feed only in the metalimnion during the night and to remain near the bottom during the day. Not all of the metalimnion can be used by mysids owing to temperature and light constraints (Beeton 1960; Teraguchi et al. 1975; Beeton and Bowers 1982; Nero and Davies 1982). Mysids migrating from the hypolimnion rarely enter water >16–17°C (Beeton 1960; Nero and Davies 1982). In 1990, the 17°C isotherm fluctuated about 15 ± 3 m (mean ± SD) depth throughout the stratified period at station 41. We considered the maximum light intensity at which *Mysis* would occur, to be that at the leading edge of the mysid migration (0.014–0.063 lx; Teraguchi et al. 1975). We have no direct measurements of moonlight, however, under the conditions of full moonlight at zenith (0.267 lux; Bond and Henderson 1963) and greatest water clarity during the stratified period (extinction coefficients of 0.19–0.23, June–July data 1989–92; E.S. Millard, Fisheries and Oceans, Burlington, ON, personal communication), these critical light intensities would be found at depths of 6–16 m. Therefore, we assumed that the upper boundary of the mysid distribution was 15 m depth at all times. The lower boundary was set by the bottom of the metalimnion, which fluctuated about 24 ± 2 m depth.

Caloric Requirements Estimated by Bioenergetic Modelling

We used a bioenergetics model developed for *Mysis relicta* by Rudstam (1989) for calculating the caloric demand of *Mysis* in both lakes Ontario and Michigan. The energetic equations for *Mysis* rely primarily on work by Sandeman and Lasenby (1980), Lasenby and Langford (1972, 1973), and Cooper and Goldman (1980) and assume that mysids feed solely on zooplankton. This model has been used to estimate food consumption by *Mysis relicta* in Kootenay Lake (Walters et al. 1991) and by *Mysis mixta* in the Baltic Sea (Rudstam et al. 1992).

We used the bioenergetics model to calculate energy requirements necessary to account for observed growth rates. Required inputs are specific growth, occupied temperature, caloric content of the mysids, and, for extrapolation to the whole population, mysid abundances and mortality rates. We used the caloric content of *Mysis relicta* reported by Lasenby (1971) for animals from Char Lake (5.000 kcal·g dry wt.$^{-1}$ (1 kcal = 4.18 kJ) for immature and 6.000 kcal·g dry wt.$^{-1}$ for mature animals, and assumed a dry weight to wet weight ratio of 0.15). Adare (1992) observed similar increases in lipid content of mysids during maturation in four Ontario lakes. Growth rates of mysids in Lake Ontario are from Johannsson (1992, 1995), and in Lake Michigan, from fig. 3 of Morgan and Beeton (1978). Mysid populations in Lakes Michigan and Ontario are composed of several generations and overlapping cohorts. The generation time of mysids in Lake Michigan is 16 mo, while that in Lake Ontario is 24 mo owing to the slow growth of Lake Ontario mysids through the winter. In Lake Ontario, 93%, of young are born in the spring and, therefore, the date used in the model for recruitment into the spring population was March 21. The late summer generation, which constitutes 7% of recruits, commenced on August 8. In Lake Michigan, three generations overlap: a March 21 generation composed of 47% of recruits, an August 8 generation providing 44% of recruits, and a November 1 generation, which contributed 9% of recruits (Morgan and Beeton 1978, derived from fig. 2).

Daily mean temperatures experienced by mysids were calculated for Lake Ontario from hypolimnetic and surface–metalimnetic temperatures, weighted for the number of hours of occupancy, and were assumed to be the same in Lake Michigan. We assumed mysids occupied the surface waters during the night and the hypolimnion from 1 h before dawn until 1 h after dusk. The seasonal temperature regime was constructed from weekly electronic bathythermograph (EBT) profiles taken from April until October at station 41, and from monthly average hypolimnetic temperatures (Johannsson 1992). The occupied temperature in the upper water column was considered equal to either (1) hypolimnetic temperatures when the water column was unstratified, (2) the average temperature of the top 30 m when the column was stratified but temperatures were <17°C, or (3) the mean

TABLE 1. Mean (±1 SD) daily instantaneous mortality rates of *Mysis relicta* from station 41 in Lake Ontario over the years 1984–91, and assigned values for Lake Michigan (see text). Values used in the energetics model are given when they differ from the calculated means. Rates were determined from the number of individuals present at the beginning and end of the size interval indicated, except for the 15.5- to 19.5-mm class, which was estimated through regression analysis. Lack of winter sampling precluded a more detailed analysis of the 7.5- to 13.5-mm size range. Immigration and emigration events in some years prevented the inclusion of data for all years. Values in parentheses are numbers of years.

	Mortality rate	
Size interval (mm)	Lake Ontario	Lake Michigan
3.1–7.5	0.017 346 ± 0.004 199 (5)	0.017 346
7.5–13.5	0.000 277 ± 0.000 277 (3)	0.000 277
13.5–15.5	0.003 816 ± 0.002 307 (5)	
13.5–15.5 (model value)	0.003 000	0.000 277
15.5–19.5	0.010 062 ± 0.003 871 (6)	0.023 400
15.5 (model for males only)	0.05	0.05

temperature between the 17°C isotherm and the bottom of the metalimnion when temperatures were >17°C. Daily mean temperature experienced by mysids ranged from 2.1°C in April to 7.7°C in October.

Mysid abundance estimates for Lake Ontario were based on the 1989 and 1990 biomonitoring data from station 41 with a total recruitment of 3000 young $\cdot m^{-2} \cdot yr^{-1}$ and a male to female ratio of 0.77 (O.E. Johannsson, Fisheries and Oceans, Burlington, ON, unpublished data). Lake Michigan was modeled with the same total annual recruitment to compare the effect of differences in growth rates through the winter and mortality rates between the two populations. Annual recruitment for a similar station in Lake Michigan is not known. Mortality rates for Lake Ontario were derived from the 1984–91 biomonitoring data (Table 1). The mortality rate used in the model for the 13.5–15.5 mm animals was changed from an observed mean of $0.0038 \cdot d^{-1}$ for the 1984–91 period to $0.0030 \cdot d^{-1}$ to better reproduce the 1989–90 population abundances. Recent life-history data are not available for Lake Michigan; we had to rely on information on population growth rates and size structure from the 1960s and early 1970s when alewife were still abundant. Mortality rates of Lake Michigan mysids were modified slightly from those observed in Lake Ontario to allow for the flat survivorship curve between 6 and 16 mm total length observed by Morgan (1976, cited in Sell 1982) and Carpenter et al. (1974), and for the 6% survivorship for females surviving to breed in the fifth instars (>15.5 mm total length) (Table 1). Generation time and, hence, growth rates are related to lake productivity and temperature (Morgan 1980; Berrill and Lasenby 1983; Beeton and Gannon 1991), which have not change significantly in Lake Michigan since the time of the above studies. However, mortality rates may have changed with changes in the planktivore community. Without more recent data, we assumed mortality rates had not changed.

For each generation, we used the bioenergetics model to calculate, on a daily basis, the energy requirements necessary to maintain observed growth rates both for individual mysids and for the total number of individuals in the generation. The mysid populations in each lake were then recreated from the individual generations in the proportions indicated above, maintaining a total annual recruitment of 3000 young $\cdot m^{-2} \cdot yr^{-1}$.

Consumption Rates of Individual Mysids: Lake Ontario

Caloric demands of individual mysids, calculated from the bioenergetics model for each generation, were compared with consumption rates estimated from measured clearance rates on different species of zooplankton to determine if, and when, mysids could obtain sufficient food when restricted to foraging on crustacean zooplankton in the surface waters at night.

To compute consumption from measured clearance rates, we must know the concentration and type of zooplankton present in that portion of the metalimnion accessible to mysids, the clearance rates of mysids for these zooplankton, and the duration of feeding. Zooplankton composition and abundance in the metalimnion were estimated from 0–20 m pump samples collected on a weekly basis at station 41 from April until October and filtered through a 64-μm mesh. The proportion of each zooplankton population that inhabited the 15- to 20-m layer at night was estimated from night pump or trap samples collected through the metalimnion and epilimnion on 10 occasions in 1986 and 1990 (Table 2). Abundances were extrapolated to the entire depth of the metalimnion by assuming that densities were constant from 15 to 24 m. Abundances were converted to biomass using length–mass regressions for *Bosmina* and *Daphnia*, body mass from Balcer et al. (1984) for *Polyphemus*, and average mass observed in the Great Lakes for the remaining organisms (N.H.F. Watson and B.J. Wilson, unpublished data; appendix 2 of Malley et al. 1989) (Table 2). Biomass was converted to calories by applying a conversion of 5.411 kcal $\cdot$ g dry wt.$^{-1}$ for cladocerans and 5.000 kcal $\cdot$ g dry wt.$^{-1}$ for copepods during the stratified period and 7.500 kcal $\cdot$ g dry wt.$^{-1}$ before and after stratification (Cummins and Wuycheck 1971; Wainman and McQueen 1993). In situ clearance rates of *Mysis relicta* were measured in Gull Lake by Nero and Sprules (1986) and in Lake Michigan by Bowers and Vanderploeg (1982). Because Lake Michigan rates were higher than those in Gull Lake, both sets of rates were applied in Lake Ontario to provide a range of consumption estimates (Table 3). We assumed that mysids fed on metalimnetic zooplankton for the entire night minus 2 h to allow for the ascent and descent of the migrating mysids. The seasonal changes in length of the night were determined from meteorological tables (List 1949). The number

TABLE 2. Percentage of each 0- to 20-m zooplankton population that occurred in the 15- to 20-m depth interval at night, based on nighttime samples through the epi- and metalimnion on 10 occasions (see text).

Species	Body mass (μg)	1986 Percentage below 15 m	1990 Percentage below 15 m in July	1990 Percentage below 15 m in August	1990 Percentage used in calculations
Diacyclops thomasi	3.2	20	3	22	20
Tropocyclops	1.7	30			30
Cyclopoid copepodids	1.9	25			25
Cyclopoid nauplii	0.9	50			50
Calanoid copepodids and adults[a]	5.8	45			45
Calanoid nauplii	2.8	30			30
Bosmina longirostris	1.1		20	12	16
Daphnia retrocurva	2.9		6	1	5
Eubosmina coregoni	3.3	20			20
Ceriodaphnia lacustris	2.5	10			10
Other cladocerans[b]					15

[a]*Diaptomus sicilis*, 12.3 μg; *D. oregonensis*, 9.3 μg; *D. minutus*, 4.5 μg; *D. ashlandi*, 4.1 μg; *Eurytemora affinis*, 6.6 μg; *Limnocalanus macrurus* adults, copepodids, and nauplii, 49.1, 8.0, and 0.5 μg.

[b]*E. longispina*, 1.1 μg; *D. galeata*, 19.5 μg; *Chydorus sphaericus*, 1.1 μg; *Diaphanosoma birgei*, 4.0 μg; *Holopedium gibberum*, 14.6 μg; *Polyphemus pediculus*, 15.0 μg; *Leptodora kindtii*, 14.8 μg.

TABLE 3. Mean in situ clearance rates of mysids on zooplankton for Gull Lake (Nero and Sprules 1986) and for Lake Michigan (Bowers and Vanderploeg 1982, calculated from table 1) and used in the present study.

Zooplankton category	Mean clearance rate ($L \cdot h^{-1} \cdot individual^{-1}$) Gull Lake	Lake Michigan
Cladocerans	0.700	1.050
Limnocalanus (all stages)	0.047	0.070
Copepod adults	0.237	0.237[a]
		0.070
Cyclopoid copepodids	0.138	0.371
Calanoid copepodids	0.193	0.388
Copepod nauplii	0.113	0.225

[a]The clearance rate for Gull Lake was used for cyclopoid adults in Lake Michigan because they were rare and no value was given: the *Limnocalanus* value of 0.070 was used for calanoid adults because no number was given.

of zooplankton that the mysids could consume on a particular night was then calculated as the product of specific clearance rates (Table 3), number of hours in the night minus two, and metalimnetic densities of prey species. Numbers consumed were then converted to biomass and calories.

Caloric Requirements of Mysid Populations in Lakes Ontario and Michigan

Seasonal patterns of energy demand were calculated for the whole mysid population in Lakes Ontario and Michigan. Mysid density increases with depth in the Great Lakes (Lehman et al. 1990; Johannsson 1992, 1995). To estimate energy demand within specific depth ranges we weighted the energy requirements of the standardized population from the bioenergetics model by the ratio of the mysid density within the specified depth range to the density of the modelled population. In Lake Ontario, the mean mysid densities of the three spatial cruises of the Lake Ontario Trophic Transfer Study (see above) were estimated within 50-m depth ranges and compared with the mean densities from the bioenergetics model for the same dates. In Lake Michigan, the average density from the bioenergetics model during the latter 2 wk of August (minus the new recruits, which were too small to be caught by the sampling gear) was compared with the mean of the densities observed during the same period between 1985 and 1989 by Lehman et al. (1990) at a total of 25 stations ranging in depth from 50 to >150 m. In Lake Ontario, the estimated energy requirements for the mysid population at station 41 were compared with the calories present in metalimnetic zooplankton.

Zooplankton Production

We only had data to calculate epilimnetic, not metalimnetic, zooplankton production, which may overestimate the production in the metalimnion that is available to mysids. Consequently, epilimnetic production should present a conservative assessment of the impact of mysids on zooplankton and their potential to compete with other planktivores. Zooplankton production was calculated by the egg-ratio method of Paloheimo (1974). Duplicate zooplankton samples were collected weekly at station 41 from the beginning of April until the end of October 1990. Samples were collected during the daytime with metered, vertical net hauls taken either through the epilimnion or from 20 m depth, whichever was shallower, with a 64-μm-mesh net (Johannsson and O'Gorman 1991). We could not use the 0- to 20-m pump samples to calculate production because the eggs had been

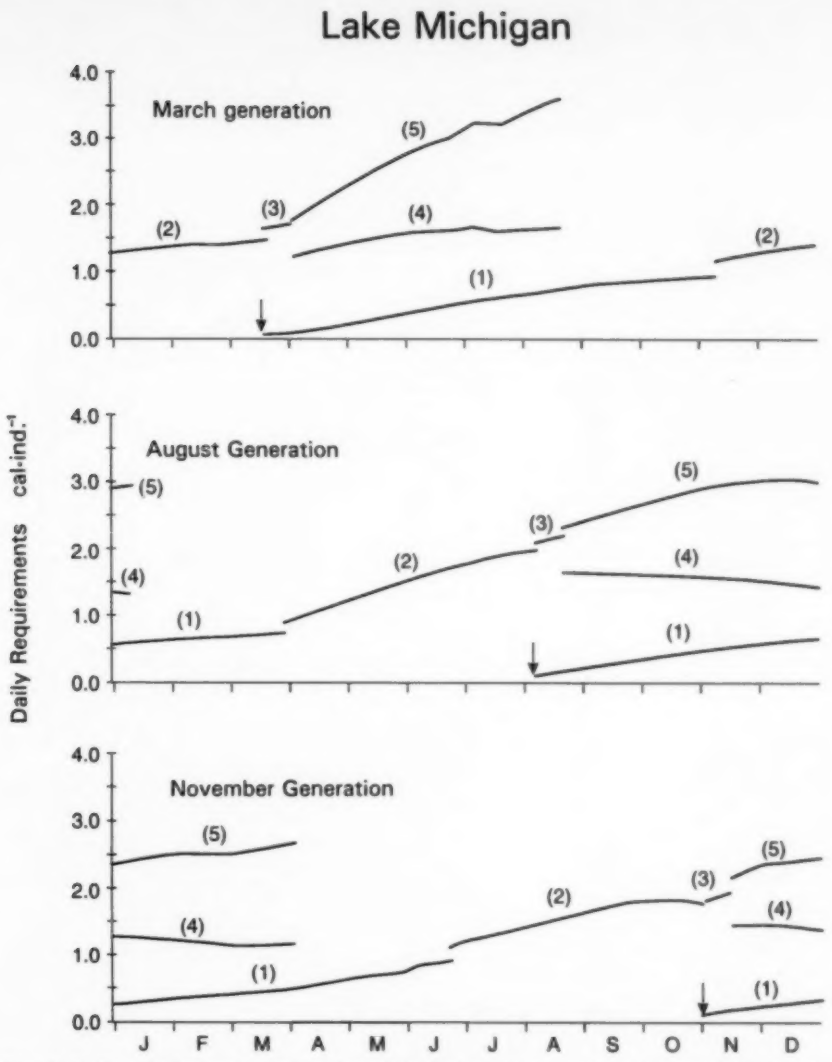

FIG. 1. Daily caloric requirements of an individual mysid through its 16 mo of life in Lake Michigan, as determined by the bioenergetics model. Three generations co-occur: each generation was modeled as five cohorts to account for changes in growth rate through the year and between sexes: steps in consumption between cohorts are associated with these differences in growth rates. Cohort numbers are indicated and arrows mark the date of birth, or first anniversary. Cohorts 4 and 5 are adult males and females, respectively.

stripped from the copepods. Only *Diacyclops thomasi* was not well represented by daytime epilimnetic samples during the stratified period (Johannsson 1987). Therefore, in July, August, and the first half of September the production of *Diacyclops thomasi* was multiplied by three to account for the under-representation of adults in daytime samples (85% of adults occurred below 15 m depth), and the growth of nauplii and copepodids, which reside principally in the metalimnion (Table 2). Average monthly production was converted to calories and compared with the caloric requirements of the mysid population from each depth range. Lastly, the mean daily calories of zooplankton production not used by mysids, if mysids feed solely on metalimnetic zooplankton, were calculated for each depth range on a monthly basis.

Results

Caloric Requirements of Individual Mysids

To model energy requirements, each mysid generation had to be broken down into a number of cohorts to take account of differences in growth rate related to season, maturation, and sex of the animals. April to October growth rates of immature and mature mysids are 0.035 and 0.029 $mm \cdot d^{-1}$, respectively, in Lake Ontario, similar to rates in Lake Michigan (Johannsson 1992). Rates decline in Lake Ontario in the winter to 0.012 $mm \cdot d^{-1}$, but not in Lake Michigan. Only female mysids appear to moult to the fifth instar and reproduce for a second time (Morgan and Beeton 1978). Males apparently die after reproducing once. For these reasons,

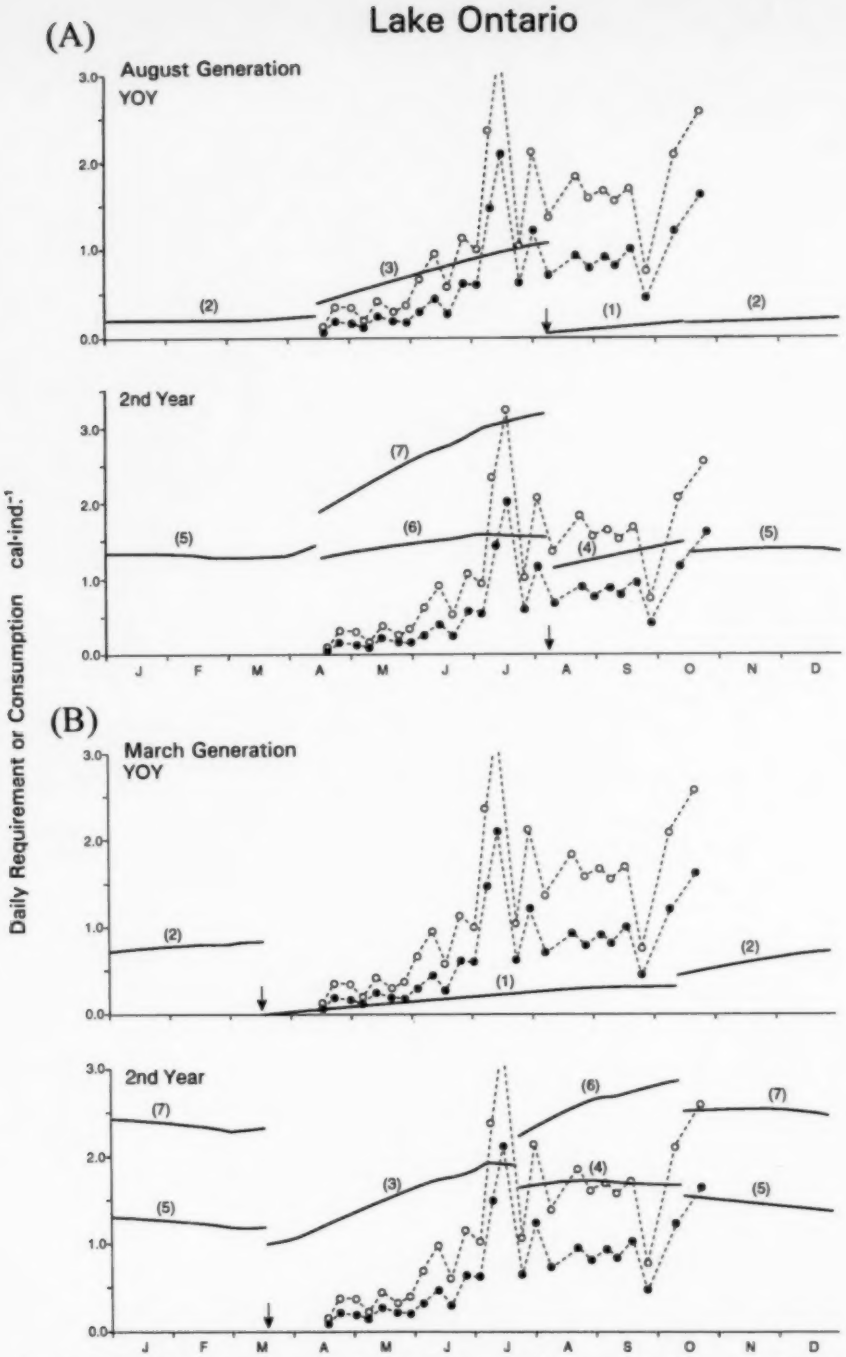

FIG. 2. Daily caloric requirements of an individual mysid through its 2 yr of life in Lake Ontario (solid line) from the bioenergetics model (A) for an animal born in the late summer (Aug. 8) and (B) for an animal born in the spring (Mar. 21). Each generation was modeled as seven cohorts. Caloric consumption was calculated from metalimnetic zooplankton densities, duration of night, and measured clearance rates of Bowers and Vanderploeg (1982) (open circles) and Nero and Sprules (1986) (solid circles). In Fig. 2A, cohorts 6 and 7 are adult males and females, respectively. In Fig. 2B, cohorts 4 and 5 are adult males, while cohorts 6 and 7 are adult females. The cohorts were split to allow for different growth rates during the winter. Other symbols as in Fig. 1.

TABLE 4. Comparison of the lifetime energy requirements of individual mysids for each generation from both lakes assuming nighttime residency in the metalimnion and consumption of zooplankton only.

Location	Generation	Energy requirements per generation (kcal · individual^{-1} · generation^{-1}) Males	Females
Lake Ontario	March	0.750	0.950
	August	0.666	0.799
Lake Michigan	March	0.533	0.709
	August	0.539	0.711
	November	0.520	0.683

seven cohorts were required to model each Lake Ontario generation, and five for each Lake Michigan generation. Daily caloric requirements increased steadily through life in Lake Michigan as a result of constant high growth rates and increased caloric density with maturation (Fig. 1). Only spent males (cohort 4) had constant or declining daily energy requirements because they were no longer growing; their requirements reflected changes in water temperature in fall and winter. Daily caloric requirements of the March generation both increased and decreased through life in Lake Ontario, the decreases being associated with lower winter growth rates as well as temperature (Fig. 2B). Mysids required 11–31% fewer calories to complete a generation in Lake Michigan than in Lake Ontario; the November Lake Michigan generation was the most efficient (Table 4). In Lake Ontario, the March generation required 13–19% more calories than the August generation because the March generation mysids were larger (>15.5 mm in length) for a larger proportion of their life: 8 mo (cohorts 4–7; Fig. 2B) as compared with 4 mo (cohorts 6 and 7; Fig. 2A).

The caloric requirements of mysids cannot always be met by nighttime feeding on the zooplankton in the metalimnion of Lake Ontario. Consumption of metalimnetic zooplankton could satisfy the caloric requirements of the August generation from August to end of October the first year and mid-June to the end of October the following summer (Fig. 2A). No zooplankton data exist for the winter period, but early spring zooplankton numbers suggest that mysid requirements during the second winter may exceed the zooplankton food source. Only the nongrowing males (cohort 6) had their caloric requirements met by consumption of metalimnetic zooplankton from July to early August the following summer. The March generation obtained sufficient energy from nighttime feeding in the metalimnion for the first 6 or 7 months of life; thereafter, demand generally exceeded potential nighttime consumption when zooplankton data were available (Fig. 2B). Only young males and females in cohort 3 (13.5–15.5 mm in length) and mature males in cohort 4 (>15.5 mm) could perhaps find enough food in the metalimnion from July until October of their second summer.

Caloric Requirements of Mysid Populations in Lakes Ontario and Michigan

The seasonal pattern and energy requirements of a mysid population in Lake Michigan differed from that in Lake Ontario, both standardized to 3000 recruits · m^{-2} · yr^{-1} (Fig. 3). The seasonal pattern was dome shaped, with high caloric requirements from April to October in Lake Ontario. This

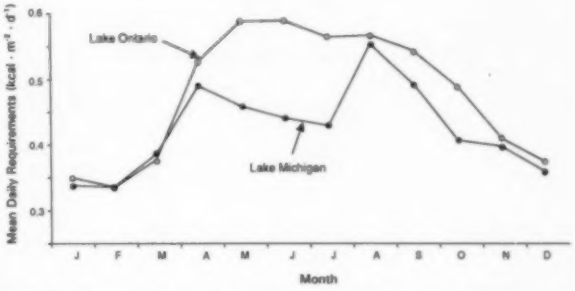

FIG. 3. Comparison of mean daily caloric requirements of mysid populations in lakes Ontario (open circles) and Michigan (solid circles). The mysid populations were standardized to 3000 recruits · m^{-2} · yr^{-1}.

coincided with the period of high growth rates in the lake. The majority of recruitment in Lake Ontario was in the spring, which reinforced the dome-shaped pattern. In Lake Michigan, energy requirements were lower than in Lake Ontario during the summer, but similar during the winter. Consequently, the overall seasonal pattern was flatter, although peaks in energy requirement occurred at times of recruitment in April and August. The density of the standardized mysid population for Lake Ontario was greater than that for Lake Michigan because generation time was 4 mo longer in Lake Ontario. Consequently, the annual energy requirement of the Lake Ontario population was 174 kcal · m^{-2} · yr^{-1} compared with 155 kcal · m^{-2} · yr^{-1} for Lake Michigan (Table 5).

Mysid density increases from nearshore to offshore and these changes greatly affect the caloric requirements of the population (Table 5). In Lake Ontario, where the major change occurred between the 50- to 100-m and 100- to 150-m depth zones, caloric requirements increased fourfold. The maximum requirement, 170 kcal · m^{-2} · yr^{-1}, occurred at depths >200 m. In Lake Michigan, energy requirements increased only 1.4 times between the 50- to 100-m and 100- to 150-m depth zones, but increased by an order of magnitude beyond 150 m to 520 kcal · m^{-2} · yr^{-1}. During the summer, the mysid population at station 41 consumed approximately 0.6 kcal · m^{-2} · d^{-1}. The total calories in the metalimnetic layer below 15 m depth ranged from 1.5 to 6.3 kcal · m^{-2}, peaking in July and remaining high until late September (Fig. 4). Demand sometimes exceeded calories present in the early spring and presumably throughout the winter. It should be noted that the density, and hence caloric demand, of the mysid population at station 41 in 1990 was exceptionally high both for its depth range and for the lake (Table 5).

TABLE 5. Comparison of densities and annual caloric requirements of mysid populations from Lakes Michigan and Ontario, assuming a nighttime distribution in the metalimnion.

Depth range (m)	Density (no. · m^{-2})		Annual caloric requirement (kcal · m^{-2})	
	Lake Ontario (LOTT mean)[a]	Lake Michigan (late August)[b]	Lake Ontario	Lake Michigan
50–100	73	82 (4)	29.720	39.589
100–150	293	113 (14)	119.294	54.590
150–200	325		132.330	
>150		1076 (7)		520.070
>200	417		169.781	
130 (station 41)	491		198.049	
Model[c]	430	306	173.727	154.645

[a]Mean of the mysid population as it was observed during the three LOTT cruises 1990: May 22–31, July 30 – Aug. 3, Oct. 29 – Nov. 9.

[b]Mean of observations, number of samples in parentheses, collected throughout the lake during last 2 wk of Aug. 1985–89 by Lehman et al. (1990).

[c]Values for the standardized population (3000 · m^{-2}) derived from the energetics model.

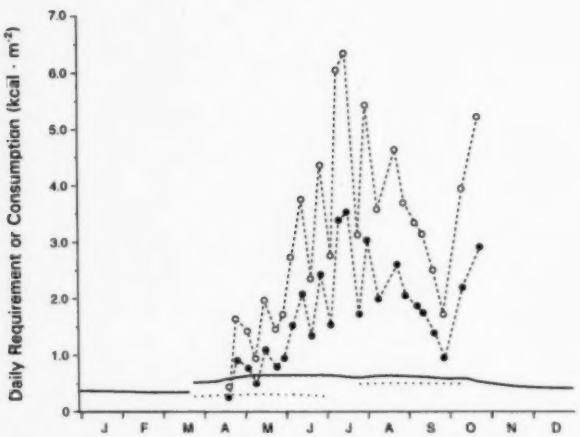

FIG. 4. Comparison of the calories required (solid line) and consumed (dotted line) by the mysid population at station 41 in Lake Ontario in 1990, and the total caloric equivalent of zooplankton present in the 15- to 24-m depth range (open circles, broken line) and the 15- to 20-m depth range (solid circles, broken line).

Comparison of Zooplankton Production and Mysid Requirements in Lake Ontario

Zooplankton were most abundant in the metalimnion from June until October (Table 6). Epilimnetic production, which we used to approximate metalimnetic production, was high from July until October, peaking in July (Table 6). Mysids required <20% of zooplankton production at depths <100 m (Fig. 5). Beyond 100 m, mysids required only 25–36% of zooplankton production in July, but 44–73% of production from August to October at depths from 100 to 200 m, and up to 109% in October at depths >200 m.

Discussion

We examined whether *Mysis relicta* could grow at observed rates in Lake Ontario when restricted to nighttime feeding on metalimnetic crustacean zooplankton, and *Mysis*' potential to sequester zooplankton production under these conditions. This feeding strategy was chosen because mysids have often been observed feeding in the upper part of the water column at night and because feeding in the metalimnion would result in the highest degree of competition for food between mysids and alewife, the dominant planktivore in Lake Ontario. Alewife are largely epi- and meta-limnetic in distribution during the stratified period (Olson et al. 1988). Comparisons of possible food intake based on clearance rates with energy requirements from bioenergetic modelling revealed that individual mysids, particularly the larger ones, could not obtain the requisite calories with nighttime feeding on crustacean zooplankton alone. Beyond 100 m depth, the mysid population was large enough (1) to exert high mortality rates on metalimnetic zooplankton, (2) to remove a significant proportion of daily epilimnetic zooplankton production, and consequently, (3) to present a potentially serious source of competition for planktivorous fish. At depths less than 100 m, the mysid population removed no more than 6–19% of zooplankton production between July and October when competition with planktivorous fish, such as alewife, would be at its maximum (Hewett and Stewart 1989; Rand et al. 1995).

The strength of these conclusions depends on the strength of the underlying assumptions and conditions in the bioenergetics model and of the assumptions and data used to calculate consumption from clearance rates. If both models were sufficiently detailed and accurate, we would expect them to provide comparable estimates of caloric intake providing that our assumption of only metalimnetic feeding on crustacean zooplankton was correct. Model estimates that diverged may indicate problems with the models or with our nighttime feeding assumption. If real, energetic model estimates that exceeded clearance rate estimates would imply that mysids feed (1) at other times of the day, (2) on other food sources in the metalimnion, and/or (3) in other more prey-rich regions during the night. Energetic model estimates that fell significantly short of clearance rate estimates would suggest that (1) mysids did not feed for the entire night or feed elsewhere on less nutritious or abundant food,

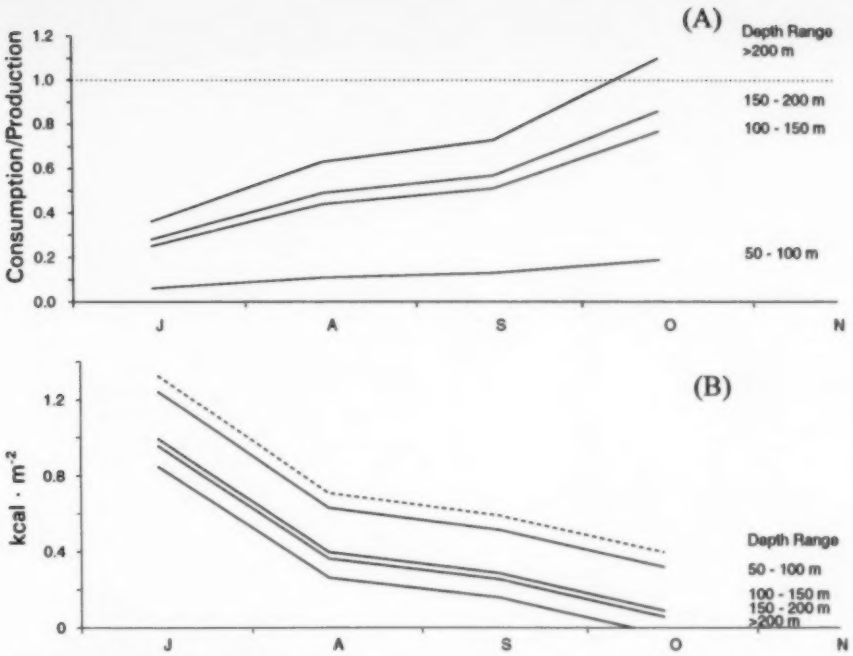

FIG. 5. (A) Comparison of the proportion of epilimnetic zooplankton production at station 41 that could be removed by the mysid population from a series of depth ranges in Lake Ontario. Dotted line shows equal production and consumption. Note that mysid density increases with depth (Table 5). (B) Comparison of epilimnetic zooplankton production at station 41, Lake Ontario (broken line), and production remaining after mysid requirements have been met (solid line).

(2) prey densities were sufficiently high that mysids became limited by handling times, or, (3) mysids interfered with each other, thereby decreasing feeding rates.

We believe the energetics model gives a reasonable estimate of the energy requirements of mysids in lakes Ontario and Michigan. Annual conversion efficiencies obtained from the model are in the order of 15% (based on energy) for the first year of life of the March generation in Lake Ontario; adults would be lower. This is lower than the 16–29% efficiency estimated by Lasenby and Langford (1973) and Hakala (1979), but these earlier energy budgets did not include any cost for standard dynamic action (see discussion in Rudstam 1989). A daily energy intake of 0.0013 kcal·d^{-1} by large mysids (Fig. 2) represents a predation rate of about 80 adult *Diacyclops* per day. Bowers and Vanderploeg (1982) observed predation rates of 115–280 prey·d^{-1} for *Mysis relicta* in Lake Michigan, and mysids from Lake Tahoe ate >100 prey·d^{-1} (Cooper and Goldman 1980).

A sensitivity analysis of the energetics model based on individual parameter perturbations showed that some changes in these parameters at the most resulted in a similar proportional change in the energy requirements (Rudstam 1989; see also sensitivity analyses of similar models by Bartell et al. 1986). The most sensitive parameters were the ones governing the temperature dependence of consumption and respiration (Bartell et al. 1986). As a consequence, the accuracy of the annual temperature regime will affect the consumption rates and conclusions we draw from them. If a solely hypolimnetic temperature regime were substituted in the model, summer consumption rates of cohorts 1, 4, and 6 of the March generation (see Fig. 2B) would have decreased by 18–24%; at most a third of the difference between the energy requirements and calories available to mysids. Summer decreases in the August generation were closer to 10%. Therefore, minor errors in temperature would not have affected the conclusions from the comparison between energy requirements and consumption.

Estimates of caloric consumption of individual mysids were based on zooplankton densities at station 41, prey caloric values from the literature and field derived clearance rates from Lake Michigan (Bowers and Vanderploeg 1982) and Gull Lake (Nero and Sprules 1986). The low lipid levels of Lake Ontario zooplankton observed by B.C. Wainman and D.J. McQueen (unpublished data) may indicate that the average caloric values taken from the literature were too high and that we have overestimated the calories available in the metalimnion. Zooplankton densities in the metalimnion were derived from 0- to 20-m pump samples by assuming a constant proportion of each population occupied the 15- to 20-m depth range. The 0- to 20-m density estimation has an error of 20–30%, while variability in proportional assignment would be 10–20% for the more abundant species. The temperature profiles indicated that the metalimnion extended to 24 m in 1990. We assumed that the density between 15 and 20 m could be extended to 24 m to calculate the total calories in the metalimnion. As density tends to decline toward the bottom of the metalimnion, the real sum of metalimnetic calories must lie between the 15- to 20-m and 15- to 24-m estimates (cf. Fig. 4). If anything, calories gained from consumption of

TABLE 6. Monthly mean metalimnetic biomass (15–24 m) and epilimnetic production of zooplankton at station 41 in 1990. Bootstrap analysis of zooplankton production estimated from replicate weekly epilimnetic samples from station 41 indicated that the coefficients of variation (COV) of the three dominant species ranged from 12 to 22% (O. Johannsson and J. Moore, Fisheries and Oceans, Burlington, ON, unpublished data). COV of the total production estimates should be similar. See text for sampling details.

Month	Metalimnetic biomass (mg dry wt.·m^{-2})	Epilimnetic production (kcal·m^{-2}·d^{-1})
April	138.2	0.031
May	197.8	0.032
June	611.9	0.085
July	890.5	1.327
August	853.3	0.709
September	497.4	0.591
October	632.2	0.396

metalimnetic zooplankton may have been overestimated. Even so, the mysid population at station 41 in 1990 required a minimum of 10–20% of the calories present in the metalimnion in late July and, at a maximum, 100% of the calories in April.

The clearance rates measured by both Bowers and Vanderploeg (1982) and Nero and Sprules (1986), and used in the present study, were averaged over the season and included a range of community structure. Therefore, they should be generally applicable to similar lakes, such as Lake Ontario. However, clearance rates are also affected by predator size (Cooper and Goldman 1980; Nero and Sprules 1986) and prey densities (Cooper and Goldman 1982; Folt et al. 1982), which were not explicitly taken into account in the present study. Small mysids take smaller types of prey and have lower clearance rates for larger prey. The clearance rate for copepods, which constitute a large proportion of the zooplankton biomass in the metalimnion, was based on data from larger mysids, which may have caused an overestimation of consumption by small mysids on crustacean zooplankton. Clearance rates are also a function of prey density above some threshold level. As long as the proportion of time spent handling a prey is short relative to the search time, the clearance rates remain constant while prey density increases. The larger the prey organism the lower the density at which handling time becomes important (Cooper and Goldman 1980; Ramcharan et al. 1985). No effects of prey density on clearance rate of a smaller copepod, *Diaptomus tyrrelli* (1.26 mm), were observed by Cooper and Goldman (1982) in experiments with densities up to 20·L^{-1}. All dominant Lake Ontario zooplankton were small (<1 mm in length; most <0.6 mm), and consequently, clearance rates should have been independent of prey densities at concentrations ≤20·L^{-1}. Prey densities in the metalimnion exceeded this level for a 2 mo period. After declining from a sharp peak of 86·L^{-1} in late July, they ranged from 23 to 46·L^{-1} in August and September, values similar to those in Lake Michigan at the time of the experiments by Bowers and Vanderploeg (1982, table 1). Therefore, the clearance rates from Bowers and Vanderploeg should be applicable to Lake Ontario. Differences between the caloric requirements of individual mysids and the estimated consumption from clearance rates were sufficiently large in the winter and spring (factor of 3 to 4), and for second-year females during the summer (factor of 1.5–2) that the above errors in the clearance rate or density estimates should have had little effect on the comparison.

We do not know if mysids can compensate for the low density of food by capitalizing on zooplankton patches to augment their consumption rates (cf. Folt et al. 1982). This would more likely occur in the summer when zooplankton are concentrated in the upper 20 m of the water column (Wilson and Roff 1973) than in winter. During the unstratified period, when mysids do not consume sufficient zooplankton to meet energy demands, the zooplankton are more dispersed through the water column. Thus, our conclusion that mysids will have to derive a significant proportion of their energy intake from sources other than metalimnetic crustacean zooplankton seems reasonable.

Mysis relicta could have obtained energy from other sources in the metalimnion, such as rotifers (Rybock 1978; Nero and Sprules 1986) and phytoplankton (Bowers and Grossnickle 1978; Grossnickle 1979). It is unlikely that rotifers significantly increased the food resources; rotifers in Lake Ontario appear to be less abundant in the metalimnion or below 15 m depth than in the epilimnion and in 1990 constituted only a small proportion of micro- plus macrozooplankton biomass in the epilimnion. The information on vertical distribution comes from the LONAS Study of seasonal distribution at a midlake site in 1982 (D. Lean, Environment Canada, Burlington, ON, unpublished data). Biomass data come from the Bioindex Program, station 41; rotifer biomass from weekly, whole-water, samples through the epilimnion during June and July constituted only 6% of total micro- plus macrozooplankton biomass, assuming a wet to dry weight conversion of 7% for rotifers (Malley et al. 1989) (O.E. Johannsson and W. Taylor, Fisheries and Oceans, Burlingtion, ON, and Universtiy of Waterloo, Waterloo, ON, unpublished data). Previous work in 1984 at station 41 indicated that rotifer abundance did not change substantially from 2 wk after stratification until the end of October, with one brief exception at the end of July (O.E. Johannsson and W. Taylor, unpublished data). As macrozooplankton biomass did not decrease through the season, rotifer contribution to total zooplankton biomass in the metalimnion throughout the year was likely small. We have no information on algal biomass in the lower part of the metalimnion. The relative importance of other food sources and daytime feeding needs to be resolved. The energy requirements predicted from the bioenergetics model were often so much larger than potential consumption of zooplankton that additional food sources must be important. Mysids can feed in both light and dark (Cooper and Goldman 1982, Ramcharan et al. 1985) and assimilation efficiency on organic material in sediments is very high (68–91%; Lasenby and Van Duyn-Henderson 1992). The ability to feed both day and night while avoiding visual predators would allow *Mysis* to shorten its generation time by maximizing its growth rate, and to survive in more oligotrophic habitats.

The generation time of mysids in Lake Michigan is shorter and hence energy transfer is more efficient than in Lake Ontario where generation time is extended by a period of slow growth in the winter. If the slower winter growth

rates were associated with a decrease in mysid energy density then winter consumption rates would be overestimated by the model. We related energy density solely to size of the mysid and not to season in the model. A loss of energy density during the winter would have to be made up over the spring and summer of the following year. This would mean a higher daily caloric requirements than predicted by the model. The necessity to recover from winter losses would affect the production of eggs in the spring and recruitment in August. This hypothesis could explain why the August generation forms only a small percentage of the mysid population in Lake Ontario but a greater percentage in Lake Michigan.

A review of the outcome of mysid introductions in North American and Scandinavian lakes highlights the strong interactions amongst planktivores, mysids, and zooplankton (Lasenby et al. 1986). In large, deep lakes, such as Ontario and Michigan, co-existence of mysids and planktivorous fish appears to be maintained through habitat partitioning and predation of fish on mysids. Planktivorous fish, such as smelt and alewife are more abundant nearshore (Wells 1968; Schaner et al. 1989; Mathers et al. 1990) while mysids are more abundant offshore (Grossnickle and Morgan 1979; Lehman et al. 1990; Johannsson 1992). In nearshore regions where planktivorous fish, such as alewife and smelt, and benthivorous fish such as slimy sculpin (*Cottus*) are more abundant, the loss rates of mysids are higher (O.E. Johannsson, unpublished data, P.S. Rand, D.J. Stewart, B.F. Lantry, L.G. Rudstam, R. O'Gorman, G. Eck, A. Goyke, S.B. Brandt, and O.E. Johannsson, unpublished data), mysid population densities are lower (Johannsson 1992) and mysids consume a smaller percentage of zooplankton production. Consumption of mysids by fish decreases their interspecific competition for zooplankton production. Mysids are further separated from alewife, the dominant planktivore in Lake Ontario, by thermal barriers during the summer when alewife consumption rates are highest (Hewett and Stewart 1989). At this time, mysids may be capturing metalimnetic production that can be used by epilimnetic and benthic planktivores if the mysids are eaten later in the year. This pathway may be most important in the nearshore (50–100 m depth) where mysids suffer heavier loss rates but are still sufficiently abundant to consume a reasonable proportion of metalimnetic calories.

By quantifying the energetics of mysids in Lakes Ontario and Michigan, we have been able to critically examine the structure and behaviour of the populations in both lakes. The differences in mysid population dynamics and energetics stem from the lower winter growth rate of mysids in Lake Ontario compared with Lake Michigan. We will understand much more about energy transfer and efficiency in these lakes when we know the underlying cause(s) for these differences in winter growth rate, their impact on caloric density and reproduction of mysids, and the selection and importance of dietary items in overcoming the apparent energy deficit.

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Size-Based Structure and Production in the Pelagia of Lakes Ontario and Michigan

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Analytical solutions to allometric models of predator–prey interactions in aquatic ecosystems indicate that normalized biomass spectra should consist of a smooth quadratic trend around which periodic oscillations occur. We confirm these assertions by showing that parabolas provide good models of normalized biomass as a function of body mass within homogeneous trophic groupings of organisms (phytoplankton, zooplankton, or fish) in the pelagic food webs of Lakes Ontario and Michigan. In addition, we show that the normalized biomass spectrum for the whole pelagic community in these lakes can be modelled by a series of parabolas of constant curvature that are aligned along a smooth quadratic base, as predicted by theory. Total secondary production in Lake Ontario is predicted from these models to be 234 kcal·m^{-2}·yr^{-1} (1 kcal = 4.19 kJ), which compares favourably with sampling estimates of about 154 kcal·m^{-2}·yr^{-1} for the whole community except rotifers and some hypolimnetic organisms, but both are higher than particle-size conversion efficiency estimates of 75–125 kcal·m^{-2}·yr^{-1}.

Les solutions trouvées par des modèles allométriques d'interactions prédacteur–proie d'écosystèmes aquatiques indiquent que les spectres de la biomasse normalisée devraient prendre la forme d'une courbe régulière du second degré modulée par des oscillations périodiques. Nous confirmons ces hypothèses en montrant que des paraboles constituent de bons modèles de la biomasse normalisée en fonction de la masse corporelle dans des groupes trophiques homogènes d'organismes (phytoplancton, zooplancton ou necton) des réseaux trophiques pélagiques des lacs Ontario et Michigan. En outre, nous montrons que le spectre de la biomasse normalisée de l'ensemble de la communauté pélagique de ces lacs peut être modélisé au moyen d'une série de paraboles de courbure constante qui suivent de près une droite de référence, transformée d'une courbe quadratique comme le prévoit la théorie. Ces modèles prévoient que la production secondaire totale dans le lac Ontario serait de 234 kcal·m^{-2}·an^{-1} (1 kcal = 4,19 kJ); ce résultat se compare favorablement aux estimations obtenues par échantillonage qui indiquent une production d'environ 154 kcal·m^{-2}·an^{-1} pour l'ensemble de la communauté à l'exception des rotifères et de certains organismes de l'hypolimnion; cependant, les deux estimations sont supérieures à celles de l'efficacité de la conversion des particules, qui sont de 75 à 125 kcal·m^{-2}·an^{-1}.

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Biomass concentration has been empirically shown to be a function of organism body size in aquatic communities (Sheldon et al. 1977; Sprules and Munawar 1986; Gaedke 1992). Such regularity in the structure of pelagic communities is predicted by allometrically based models of energy flow from prey to predators (Kerr 1974; Borgmann 1982; Dickie et al. 1987). More recently, Thiebaux and Dickie (1992, 1993) have shown that periodic components to residuals around smooth trends in biomass distributions are neither sampling artifacts nor unexplainable variation, but follow analytically from the predator–prey models. If confirmed empirically, these advances will provide a rigorous quantification of size-based predation dynamics in aquatic communities as well as a basis for prediction of potential production.

In this paper we use sampling information on the size structure of pelagic food webs in Lakes Michigan and Ontario to test the predictions Thiebaux and Dickie (1992, 1993) make about the relationship between normalized biomass and body size in aquatic communities. In addition, we use these models to show that prediction of secondary production in Lake Ontario compares favourably with independent estimates derived from cohort and egg-ratio calculations.

Materials and Methods

Lake Michigan

Detailed methods have already been published (Sprules et al. 1991) but are summarized here. The lake was sampled in both May and August–September 1987 along nine inshore–offshore transects distributed around its periphery. Phytoplankton biomass was estimated from microscopic

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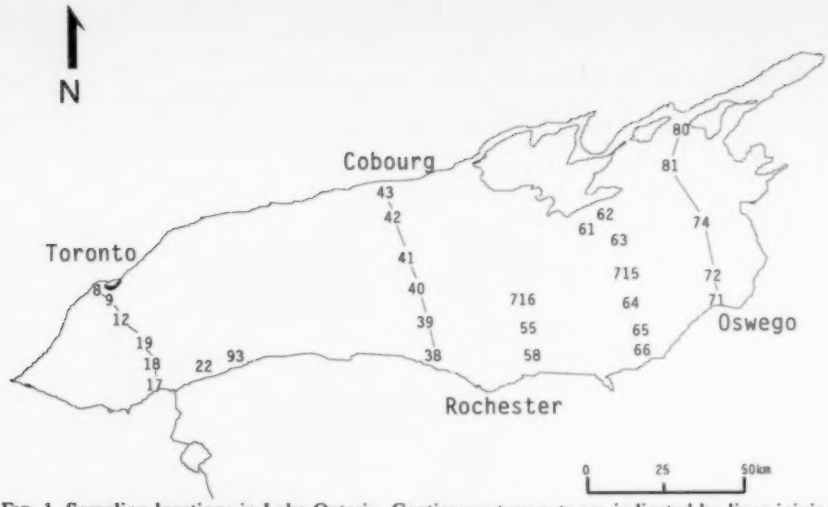

FIG. 1. Sampling locations in Lake Ontario. Continuous transects are indicated by lines joining stations. Sampling periods were May 22 – June 1 (spring), July 30 – August 3 (summer), and October 29 – November 8 (fall) 1990.

examination of samples taken through the photic zone with an integrating sampler (Schroeder 1969). Zooplankton was collected by vertical hauls of a 110-μm tow net, and identified and measured microscopically. Biomass was determined from published length–weight relationships. Planktivorous fish density was sampled with a 120-kHz dual-beam echosounder towed continuously at night along the transects (Brandt et al. 1991). Fish density was converted to biomass on the basis of bottom-trawl samples that gave species and size composition. Piscivorous fish density and biomass were determined from bioenergetic growth models (Stewart and Ibarra 1991), which balance consumption with metabolic losses for stocked cohorts of known abundance and measured growth increment. These data were used to compute fresh biomass per $\log_2$ body-size interval ($g \cdot m^{-2}$) for all trophic groups.

Lake Ontario

Data for Lake Ontario were collected on three research cruises (conducted in spring, summer, and fall 1990) (Fig. 1). Organisms were sampled as follows. Autotrophic picoplankton (fluorescence microscopy) and bacteria: stations 8, 12, 17, 19, 38, 41, and 43 in summer and stations 12, 17, 19, 64, and 66 in fall. Heterotrophic nanoflagellates: same as above except not stations 12, 41, 64, and 66. Phytoplankton: all of western and central transect stations in spring and summer; stations 9, 17, 18, 19, 38, 39, 42, 43, 71, 72, 80, and 81 in fall. Zooplankton: stations 9, 12, and 17 in summer and fall; stations 38, 41, and 43 in all periods (except station 40 rather than 43 done in fall); and stations 71, 74, and 81 in spring and fall. Ciliates: all western, central, and eastern transect stations in all periods (except not station 9 in summer); stations 61–66 (excluding station 715) in spring and fall. *Diporeia*: western transect stations except 17, stations 38–40, 63–65 (including 715), 72–80, 8, 22, 93, 55, 58, and 716 in fall. Fish: western transect and central transect from station 41 north in summer; western, central, and eastern transects in fall.

Phytoplankton biomass and species composition were determined from microscopic examination of integrated water-column samples taken during the day from the surface to 20 m (or to 2 m above bottom). Samples fixed with Lugol's preservative were examined under a light microscope for all autotrophs including picoplankton, species were identified, and cell dimensions measured so biovolumes could be computed (Munawar et al. 1974). Samples fixed in 1.5% formaldehyde and stained with DAPI (4′,6-diamidino-2-phenylindole) were examined under green and UV epifluorescence illumination (M. Legner, Department of Fisheries and Oceans, Burlington, ON) to enumerate and measure bacterial cells, autotrophic picoplankton (as a check on direct counts), and heterotrophic nanoflagellates (Weisse and Munawar 1989). Ciliates were enumerated and measured (P.L. Humby-Searle, University of Guelph, Guelph, ON) using light microscope analyses of aliquots of the Lugol samples treated with Bouin's solution and protargol stain (Montagnes and Lynn 1987). Ciliate biovolumes were determined from geometric models of the various species.

Zooplankton was sampled at night with a 50-cm, 110-μm mesh metered tow net hauled from 100 m (or 3 m above bottom at shallower stations) to the surface, and with a 30-cm, 41-μm metered net hauled from 30 m (or 3 m above bottom). Samples preserved in buffered formaldehyde were analyzed under a microscope fitted with a video camera and monitor, organisms identified to functional group (Sprules and Jin 1990), body lengths measured with digitizing calipers (Sprules et al. 1981), and body mass (fresh weight) determined from published length–mass regressions. Only a few of the 41-μm net samples were processed to determine how much the coarser net underestimated the biomass of small rotifers.

Diporeia hoyi (Crustacea: Amphipoda) biomass was estimated from Ponar samples that were screened through 4-, 1-, 0.58-, 0.25-, and 0.15-mm sieves (R. Dermott, Department of Fisheries and Oceans, Burlington, ON, personal communication). These amphipods appear regularly in the diets of planktivorous fish (MacDonald et al. 1990). All retained *D. hoyi* on each sieve, or subsamples if volume required, were enumerated, total preserved fresh mass determined to 0.01 mg, and mean individual body mass

computed by dividing total mass by numbers. Data from all five sieves were combined to give total abundances in a range of body mass categories.

Fish density and length were determined by continuously towing a downward-looking 120-kHz dual-beam acoustic system along the sampling transects at night (Brandt et al. 1991). Planktivorous fish species composition (principally alewife, *Alosa pseudoharengus*, and smelt, *Osmerus mordax*) body masses were determined from periodic midwater and bottom trawls. Piscivore mass–length relationships were also determined from fresh specimens (principally chinook salmon, *Oncorhynchus tshawytscha*, coho salmon, *O. kisutch*, rainbow trout, *O. mykiss*, brown trout, *Salmo trutta*, and lake trout, *Salvelinus namaycush*). Biomass concentrations were averaged over the whole water column along a complete transect.

For all trophic groups, biomass concentration was expressed as grams per square metre (fresh weight). To construct an unnormalized biomass size spectrum, a scale of body mass in which each interval is double the previous was established (this scale is arbitrary but was chosen to be consistent with previous analyses). Organisms from all trophic groups were then placed in the appropriate size interval and the total biomass in each interval computed (see Fig. 2 for example). The normalized size spectrum differs only in the ordinate, which is a logarithmic scale of biomass ($g \cdot m^{-2}$) divided by the width of the body mass interval (g) with resultant units of $\log(m^{-2})$ (see Fig. 7 for example). In this paper we deal only with spectra averaged over all time and space samples to capture the principal structural features of the pelagic community without its spatial and temporal dynamics. It should be noted that the various trophic groups were not all sampled at the same time and place.

Size Spectrum Model

A generalized model of energy flow from prey population i to predator population j is given by

$$(1) \quad M_j = \left(\frac{M}{P}\right)_j K_j F_j M_i$$

where M = biomass, P = production, K = gross production efficiency, and F = the proportion of prey i captured that are a fraction R the size of their predators (Boudreau et al. 1991). P/M and KF are both allometric functions, i.e.,

$$(2) \quad \frac{P_j}{M_j} = a' w_j^{\gamma}$$

$$(3) \quad K_j F_j = a'' w_j^{\gamma'}$$

where w is body mass. From these equations it follows that

$$(4) \quad \frac{B_j(w)}{B_i(Rw)} = \left(\frac{a''}{a'}\right) w^{\gamma''-\gamma'}$$

(Thiebaux and Dickie 1993). Here w is body mass and $B_n(w)$ is the normalized biomass function giving biomass concentration per unit body size within an interval centred on w. If predators and prey are in the same trophic group (e.g., large and small fish), then the subscripts in the above equations are dropped, and Thiebaux and Dickie (1992, 1993) show that the solution of Equation (4) gives $\log B$ as a quadratic function of $\log w$ plus a periodic function in $\log w$. The quadratic function or parabola follows from the predator–prey interactions and their allometric features embodied in Equations (1)–(4), and the periodic component follows from the premise that predators in aquatic ecosystems feed on prey that are smaller by the fixed ratio R.

Similarly, if predators and prey are in different trophic groups (e.g., fish feeding on zooplankton) the solution to Equation (4) shows how a biomass function $\log B_n$ is related to the biomass function in a neighbouring trophic position. Each function has a peak corresponding to the biomass dome of a component trophic grouping, and the relative positioning of the peaks as governed by Equation (4) corresponds to the overall parabolic or smooth decreasing trend in normalized biomass across all organisms in a community (see Fig. 7 for example). The solution indicates that the domes have identical shapes if and only if they are parabolas, and are shifted horizontally and vertically in a predictable fashion, making it possible to predict normalized biomass in any dome given knowledge of it in a particular dome (Thiebaux and Dickie 1992, 1993).

To test these assertions, we fit quadratic functions to each of the phytoplankton, zooplankton, and fish trophic groups for annual, lakewide normalized biomass spectra for both Lakes Michigan and Ontario. We removed the heterotrophic nanoflagellate and bacterial biomass from Lake Ontario to make the two data sets comparable (this amounts to only 1.8% of the total phytoplankton biomass). Curve fitting was done with SigmaPlot® Curve Fitter (Kuo et al. 1992) which uses the Marquardt–Levenberg algorithm (Press et al. 1986). To test differences in quadratic parameters among trophic groups statistically, we established the frequency distribution of pairwise differences (i.e., phytoplankton–zooplankton, zooplankton–fish, etc.) for a given parameter by bootstrapping the observed data 2000 times, and then determined the two-tailed probability interval within which the null difference of 0 fell (Manly 1991). A separate randomization was done for each comparison; hence, no Bonferroni adjustment was required. To be consistent with units in Thiebaux and Dickie (1993), we converted our units of fresh grams per square metre to kilocalories per square metre using factors of 1.3 for fish and 1.0 for phytoplankton and zooplankton (Boudreau and Dickie 1992).

Results

The size structure of the Lake Ontario pelagic community (Fig. 2A) is composed of three major "domes" of biomass corresponding to phytoplankton, zooplankton, and fish. Each dome incorporates secondary peaks reflecting, for instance, a spring bloom of the diatom *Melosira* (large peak at right of algae dome), and the pelagic amphipod *Diporeia*. Ciliate biomass, too low to illustrate, averages $0.49\ g \cdot m^{-2}$ spread out over roughly 10 size classes in the right half of the algal peak. As much as 60–70% of the rotifer biomass may be missing because of the coarse (110-μm) plankton net used, but this would only be about 4% of the total zooplankton biomass.

The structure of the Lake Michigan pelagic community (Sprules et al. 1991; Fig. 2B) is similar in that it too is composed of three biomass domes corresponding to the major trophic groups. Although spring diatom blooms occur in Lake Michigan (Bowers et al. 1986), they do not reach the high densities typical of Lake Ontario. Of particular note

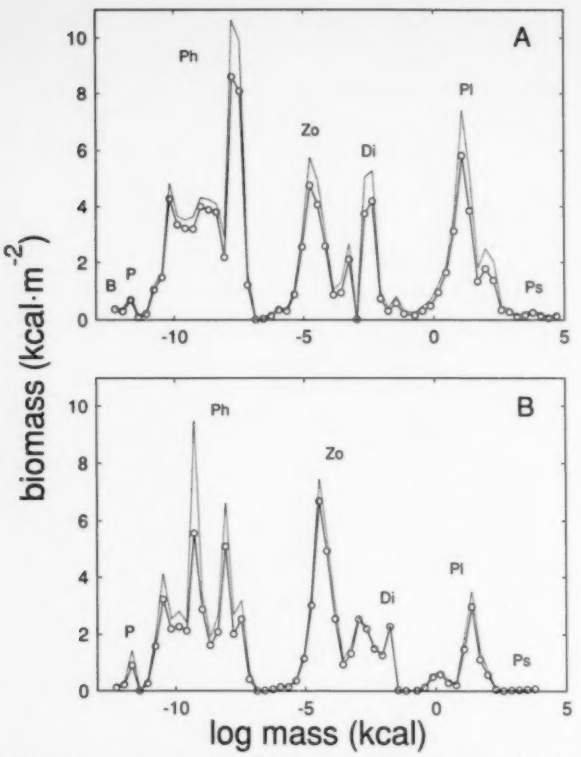

FIG. 2. Mean unnormalized biomass size spectrum for (A) Lake Ontario and (B) Lake Michigan. Circles and solid lines are means for individual size groups; dotted line is one standard error above means. B = bacteria; P = picoplankton; Ph = phytoplankton; Zo = zooplankton; Di = *Diporeia*; Pl = planktivorous fish; Ps = piscivorous fish. The bottom panel is modified from Sprules et al. (1991, fig. 7).

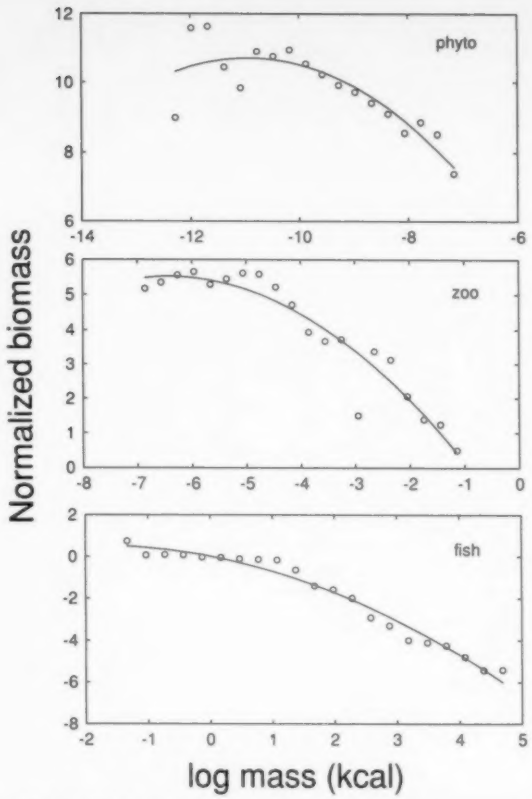

FIG. 3. Modelled parabolas (lines) for normalized biomass (circles) of Lake Ontario trophic groups. See Materials and Methods for description of normalized biomass value calculation.

is the larger biomass peak of planktivorous fish, principally alewife, in Lake Ontario (Fig. 2A). Displacement of the principal zooplankton biomass peaks (Fig. 2) reflects the predominance of small-bodied zooplankton (rotifers, bosminid cladocerans, and cyclopoid copepods) in Lake Ontario in contrast to Lake Michigan where *Daphnia* and calanoid copepods are abundant. This is almost certainly due to the greater planktivore biomass in Lake Ontario that consists of roughly 79% alewife and 21% smelt. In Lake Michigan, 72% of the planktivores are bloater, *Coregonus hoyi*, (Sprules et al. 1991), which live in deeper, colder water than alewife and, hence, feed less intensively on epilimnetic zooplankton.

Model Evaluation within Trophic Groupings

The assertion by Thiebaux and Dickie (1992, 1993) that normalized biomass within trophic groups is a quadratic function of log mass is confirmed for both Lakes Michigan and Ontario (Fig. 3 and 4; Table 1). In all cases the mean-square error of the quadratic model is smaller than that for a linear model. Residual variation around the parabolas is greatest for phytoplankton (Table 1) owing principally to deviations from the fitted curves in the smallest size classes of algae, possibly reflecting uncertainty in sampling estimates of these organisms. Variability around the smooth parabolic trends is also a reflection of temporal and spatial dynamics in the community and possibly of external perturbations, such as contaminant loading.

It should be recalled, however, that oscillations around the domes within a trophic group are to be expected from predator–prey interactions within those groups (Thiebaux and Dickie 1993). An examination of residual variation around the trophic domes for both lakes reveals clear periodic structure within zooplankton and fish (Fig. 5 and 6). These peaks are the size groups of organisms making up the major trophic groupings. The fish trophic group, for instance, comprises large predatory salmonids and their smaller prey (primarily alewife and smelt). In both lakes there is the suggestion of a third peak of very small fish, which are the young-of-the-year planktivores (Fig. 5 and 6). Within the zooplankton trophic group, a similar diversity of predator–prey pairs such as the large hypolimnetic predator *Mysis* feeding on mid-size zooplankton (*Daphnia* and copepods), and midsize cyclopoid copepod predators feeding on small cladocerans and rotifers, is manifested as three component peaks (Fig. 5 and 6). These secondary periodic structures superimposed on principal domes reflect the fact that aquatic food webs comprise larger predators feeding on prey located at roughly constant intervals down the body-size continuum (Thiebaux and Dickie 1993). Periodic structure is much less clear within phytoplankton, suggesting predator–prey relationships within this trophic group are

Table 1. Parameters (with standard errors given in parentheses) estimated for the within trophic group model by fitting the parabola $y = a + 0.5c(x - b)^2$ to the normalized biomass spectrum for individual trophic groups where y is normalized biomass (log (m^{-2})) and x is log mass (kcal), c is curvature of the parabola, and a and b are the y- and x-coordinates of the vertex, respectively. The standard deviations of the regressions and vertical and horizontal shifts of the vertices of the domes from one trophic group to another are shown. Probabilities are from bootstrapping tests of no differences among indicated parameters.

	Phytoplankton	Zooplankton	Fish	*P*
Lake Ontario				
c	−0.44 (0.13)	−0.37 (0.09)	−0.30 (0.05)	0.7, 0.31, 0.67[a]
a	10.71 (0.20)	5.52 (0.25)	0.54 (0.29)	
b	−10.93 (0.42)	−6.41 (0.63)	−1.86 (0.62)	
SD_{regr}	20.9	9.04	4.36	
Vertical shift	−5.2	−5.0		0.67
Horizontal shift	5.5	4.6		0.95
Lake Michigan				
c	−0.29 (0.11)	−0.57 (0.07)	−0.43 (0.16)	0.09, 0.58, 0.44[a]
a	11.25 (0.34)	5.24 (0.12)	−0.16 (0.52)	
b	−12.35 (1.04)	−5.38 (0.18)	−1.15 (1.03)	
SD_{regr}	8.96	3.52	5.07	
Vertical shift	−6.0	−5.4		0.20
Horizontal shift	7.0	4.2		0.07

[a]Tests of differences for phytoplankton–zooplankton, zooplankton–fish, and phytoplankton–fish, respectively.

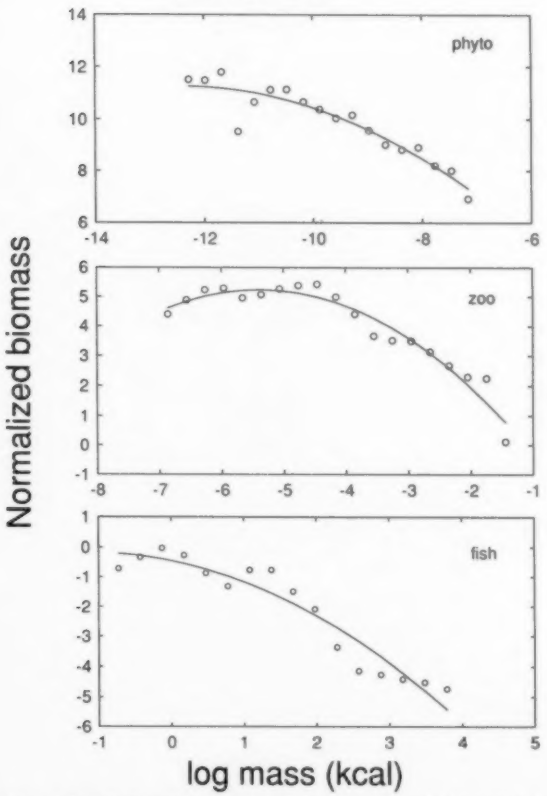

FIG. 4. Modelled parabolas (lines) for normalized biomass (circles) of Lake Michigan trophic groups.

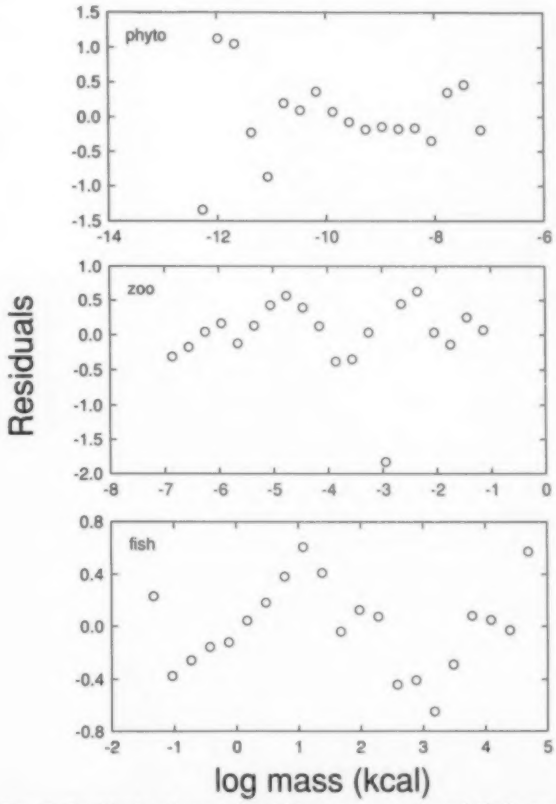

FIG. 5. Residuals of normalized biomass around modelled parabolas for trophic groups in Lake Ontario.

less structured than within zooplankton and fish. Weaker links or larger prey–predator size ratios, such as between algae and Protozoa (which fall into the phytoplankton size range) and between picoplankton and heterotrophic nanoflagellates may contribute some residual periodic structure to the algal dome.

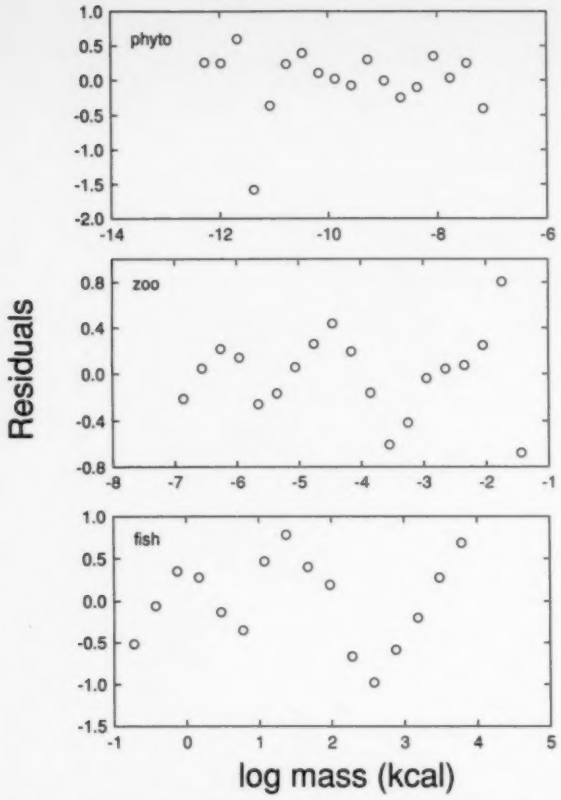

FIG. 6. Residuals of normalized biomass around modelled parabolas for trophic groups in Lake Michigan.

Parabola curvature, $c_o = (\tau' - \tau'')/\log R$, (Thiebaux and Dickie 1993), is determined by predator production and foraging functions (the τs, see Equations (2) and (3)) as well as by the ratio of prey–predator size (R). Because parabola curvature is invariant (Table 1), it is implied that these ecological parameters do not vary among trophic groups, or else vary in a way that keeps the above relationship constant. Visual inspection of Fig. 5 and 6 indicates that separation among predator–prey pairs for within zooplankton and fish is constant at roughly two logarithmic mass units, and Dickie et al. (1987) show that τ', the exponent in the specific production – body size relationship, varies minimally among trophic groups (see also Table 2). These observations imply that τ'', the exponent in the relationship between combined capture and production efficiencies and body size, is also the same for all trophic groups. There is a numerical difference in τ'' for zooplankton from our study and fish from another study (Table 2), but too few data are currently available for further evaluation of these relationships (Thiebaux and Dickie 1993).

Model Evaluation among Trophic Groupings

The solution to models for predation between trophic groups (e.g., fish feeding on zooplankton) and, hence, patterns in normalized biomass for the whole community is slightly different. Thiebaux and Dickie (1992, 1993) predict that normalized biomass for a whole pelagic community should be a smooth quadratic function of log mass along which biomass domes of component trophic groupings are positioned. If the domes are modelled as parabolas, and if R is fixed, then the normalized biomass spectrum should be composed of a series of parabolas of fixed curvature and uniform vertical and horizontal displacement. We found there were no statistical differences among curvatures or in horizontal and vertical displacements of the trophic domes for either Lake Ontario or Lake Michigan (Table 1) indicating agreement with Thiebaux and Dickie's (1993) prediction. Thus, as a final description of normalized biomass, we iteratively sought the single estimate of parabola curvature for each lake that would give the best overall fit of three parabolas to the component trophic groupings and also fit a quadratic trend through the whole biomass spectrum (Table 3; Fig. 7). These are the smooth quadratic trends and regularly placed biomass domes predicted by Thiebaux and Dickie (1993). It is interesting to note (Table 3) that the overall quadratic trend is close to linear, and that the parameters of the linear term (−1.09 and −1.14 for Lakes Ontario and Michigan, respectively) are close to those reported in other studies (Boudreau et al. 1993).

Table 2. Parameter values for Lake Ontario zooplankton derived from the parabola of log normalized biomass (log (m^{-2})) as a function of log mass (Thiebaux and Dickie 1993). $\gamma = \gamma'' - \gamma'$, and $a = a''/a'$ (see text, Equations (2) and (3). Values for freshwater fish from a small lake (Thiebaux and Dickie 1993) are shown for comparison. Standard errors are given in parentheses.

Parameter	Zooplankton	Fish
c_o[b]	−0.37 (0.09)	−0.67 (0.12)
log w_o[c]	−6.41 (0.63)	−0.81 (0.20)
log B_o	5.52 (0.25)	−0.45 (0.18)
log R[d]	−2	−3
γ'	−0.31 (0.14)	−0.29 (0.11)
γ''	−1.05	−2.29 (0.39)
log a'	−0.18 (0.66)	0.47 (0.17)
log a''	−4.18	1.85

[a] $\log B(w) = \log B_o + 0.5c_o(\log w - \log w_o)^2$.
[b] $c_o = -\gamma/\log R$.
[c] $w_o = R^{0.5/a^{1/\gamma}}$.
[d] Estimated from inspection of Fig. 5; R is the prey–predator size ratio.

Production Calculations

To illustrate an application of these models, we derive an estimate of annual zooplankton production for Lake Ontario using the within trophic group parameters (Table 1). Borgmann (1983) and Borgmann et al. (1984) provide data on body size and production:biomass ratios for *Mysis* in Lake Ontario in 1971 and a variety of crustacean zooplankton species in 1981. We used these data to derive values for the parameters in the allometric production relationship (Equation (2)) a' and γ' to be 0.661 and −0.31, respectively, the latter being typical of such values for other trophic groupings of organisms (Banse and Mosher 1980). These values, in combination with parameters of the parabola of normalized zooplankton biomass (Table 3), allow a complete parameterization of biomass and production processes

TABLE 3. Parameters (with standard errors given in parentheses) estimated for the among trophic group model by fitting parabolas of fixed curvature, c, to component domes in the normalized biomass spectrum for Lakes Ontario and Michigan (see text). Parameters of a parabola fit to the overall size spectrum are also shown. Other symbols as in Table 1.

	Phytoplankton	Zooplankton	Fish	P	Overall
Lake Ontario (SD_{regr} = 12.6)					
c	−0.35	−0.35	−0.35		−0.024 (0.009)
a	10.69 (0.20)	5.55 (0.22)	0.37 (0.15)		25.2 (8.5)
b	−11.25 (0.26)	−6.53 (0.22)	−1.40 (0.12)		−45.8 (17.0)[a]
Vertical shift		−5.1	−5.2	0.94	
Horizontal shift		4.7	5.1	0.43	
Lake Michigan (SD_{regr} = 13.2)					
c	−0.45	−0.45	−0.45		−0.024 (0.01)
a	11.09 (0.18)	5.19 (0.13)	−0.21 (0.28)		27.31 (10.3)
b	−11.43 (0.18)	−5.72 (0.12)	−1.04 (0.21)		−48.3 (19.9)[a]
Vertical shift		−5.9	−5.4	0.21	
Horizontal shift		5.7	4.7	0.05	

[a]Value of the x parameter when quadratic simplified to $y = d + ex + fx^2$ is −1.01 and −1.14 for Lakes Ontario and Michigan, respectively.

in Lake Ontario zooplankton, which are listed with those derived for fish in a small lake (Thiebaux and Dickie 1993) for comparative purposes (Table 2). For the $\log_2$ body-mass intervals we have used (Fig. 3), normalized biomass in an interval centred on size w_i is $B(w_i) = M(w_i)/w_l$, where $M(w_i)$ is unnormalized biomass in the interval and w_l is the lower boundary of the interval. Rearranging Equation (2), substituting the quadratic equation for normalized biomass (Table 1), and using specific parameters gives

$$\log P(w_i) - \log M(w_i) = \log a' + \gamma' \log w_i$$

$$\log M(w_i) = \log B(w_i) + \log (w_l)$$

$$\log P(w_i) = 5.52 - 0.185(\log w_i + 6.41)^2 + \log w_l - 0.18 - 0.31 \log w_i$$

where $P(w_i)$ is total production (kcal · m^{-2} · yr^{-1}) in the size interval centred on w_i. Summing these productions up across all zooplankton size intervals in Lake Ontario gives total zooplankton production of 234 kcal · m^{-2} · yr^{-1}. This value represents the annual production of combined rotifers, crustaceans, *Mysis*, and *Diporeia*, the organisms included in the size range of the zooplankton dome. For comparison, direct measurement of production for only epilimnetic crustaceans (no rotifers, *Mysis*, or *Diaporeia*) is 97.6 kcal · m^{-2} · yr^{-1} for April–October 1990 (Johannsson et al. 1994) or 153.8 kcal · m^{-2} · yr^{-1} for the whole year including *Mysis* and *Diaporeia* (Lake Ontario Committee 1992), and is 150.2 kcal · m^{-2} · yr^{-1} for epilimnetic crustaceans for the whole year in 1981 (Borgmann et al. 1984). Given that none of these estimates includes production of rotifers or hypolimnetic species, such as the calanoid copepod *Limnocalanus*, the value of 234 kcal · m^{-2} · yr^{-1} estimated from the normalized biomass model appears reasonable.

Borgmann (1982) shows that it is possible to compute production for any size range of organisms if production of some other size group is known and if the value of ε, the particle-size conversion efficiency, is known. Following the approach of Sprules et al. (1991), we used an estimate of 1904.7 kcal · m^{-2} · yr^{-1} for 1990 annual photosynthesis in Lake Ontario (S. Millard, Fisheries and Oceans, Burlington, ON, personal communication), the size ranges of algae and zooplankton from Fig. 2A, and typical values of ε for Lake Ontario of 0.22 and 0.26 (Borgmann 1982), to independently estimate annual production of all zooplankton at 75.0–125.0 kcal · m^{-2} · yr^{-1}. These are overestimates because

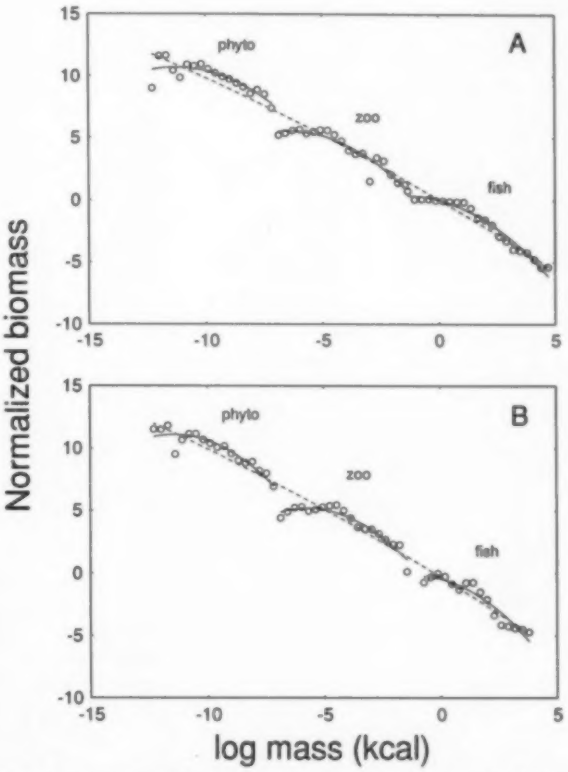

FIG. 7. Parabolas of fixed curvature (lines) fit to normalized biomass (circles) for individual trophic groups in (A) Lake Ontario and (B) Lake Michigan. Broken lines are parabolas fitted to the overall biomass spectrum (see Table 3).

they are based on gross primary production (photosynthesis) rather than net production, yet they are still lower than measured values that do not even include all zooplankton.

Discussion and Conclusions

The analytical solution to the general model of energy flow between predators and prey in aquatic communities (Equation (1)) is that normalized biomass is a periodic function of log mass superimposed on a smooth quadratic base (Thiebaux and Dickie 1992, 1993). If one considers structure within a trophic grouping, such as fish, then normalized biomass as a function of log mass should form a parabolic dome of biomass with periodic residual variation around this parabola. We have confirmed this for Lakes Ontario and Michigan (Fig. 3 and 4). On the other hand, if one considers structure across major trophic groupings, then normalized biomass for a whole community should consist of a series of repeated structures superimposed on a quadratic base. The precise shape of the periodic structures does not follow from the mathematics but we have taken them to be parabolas following Thiebaux and Dickie (1993). Offset parabolas of uniform curvature provide a good description of normalized biomass in both lakes. Whether the within- or between-trophic-grouping perspective is adopted depends on the goal of the particular analysis. Characterization of the structure of a whole community and prediction of normalized biomass for any size range of organisms given information for a particular size range would suggest a focus on the across-group formulation. By contrast, interest in quantifying the parameters of predator–prey interactions within trophically homogeneous groups of organisms (e.g., zooplankton) would suggest a focus on the within-group formulation.

The important inference of these models is that specific structural features of the normalized biomass size spectrum follow directly from allometric formulations of predator–prey interactions in aquatic communities, and we have empirically confirmed these expectations. Sheldon et al. (1977) originally proposed that normalized biomass spectra were smooth linear functions. Debate about the "smoothness" or "jaggedness" of such spectra has tended to focus on variation around a linear trend as being caused by sampling artifacts or perturbations (Sprules and Munawar 1986; Gaedke 1992). As Thiebaux and Dickie (1993) observe, the task now would be to explain why any observed spectrum does not show periodic or repeated structure. Overall Thiebaux and Dickie's (1993) formulation provides an alternative approach to those of Sheldon et al. (1977) and Borgmann (1992) as a basis for making predictions about biomass concentration for particular size ranges of organisms given data on other size ranges, and ultimately for deriving estimates of potential production.

An estimate of zooplankton production for Lake Ontario based on the within-group model described here appears reasonable in comparison with independent population-based estimates. This estimate required information on both normalized biomass parabola parameters and the allometric *P/M* relationship for zooplankton. If parabola parameters for other trophic groups are predictable from zooplankton, as appears to be the case for Lakes Ontario and Michigan, then other production estimates require only information on the associated *P/M* relationship. Given general trends in this relationship (Banse and Mosher 1980; Boudreau et al. 1991), a first approximation may be possible without direct measurement. Estimates of secondary production in Lake Ontario based on Borgmann's (1982) particle-size conversion-efficiency formulation were much lower than sampling estimates or the within trophic group model of Thiebaux and Dickie (1993). This suggests either that estimates of conversion efficiency for Lake Ontario are too low or that Borgmann's (1982) model has limitations, but additional data are required for evaluation. It is certainly worth pursuing size-based models of biomass and production in aquatic communities as alternatives to population-based approaches.

Acknowledgements

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Application and Future Potential of Statolith Increment Analysis in Squids and Sepioids

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Periodic increments within the squid statolith microstructure are now routinely used to obtain individual age estimates. Validation and culture studies have shown that statolith increments (similar to increments in larval fish otoliths) are produced daily in a number of squid species and in one sepioid. However, sample sizes for validation studies are small and there is need for further, more comprehensive validation experiments. Statolith age analysis has revealed that temperate squids can complete their life cycle in less than 2 yr while tropical species live for less than 8 mo. Obtaining individual age estimates has also facilitated the identification of cohorts by analysing hatch date distributions. Size-at-age analysis has been used for some preliminiary growth modelling, and there is a continued need for more accurate age-based squid growth models. There is now potential to use image analysis systems for increment counts and for width analysis of increments. Future studies should be aimed at obtaining age information from a wider number of species, considering how other features within the statolith microstructure, such as zones, might reflect past habitats, and determining how statolith length or weight measurements might be related to past growth histories.

Les accroissements périodiques de la microstructure des statolithes du calmar sont maintenant couramment employés pour estimer l'âge des individus. Des études de validation et des cultures ont montré que les accroissements des statolithes, qui sont semblables à ceux des otolithes des larves de poissons, se produisent quotidiennement chez un certain nombre d'espèces de calmar et chez un sépioïde. Cependant, les tailles d'échantillons utilisées dans les études de validation sont faibles et des études plus poussées de validation sont nécessaires. La détermination de l'âge par les statolithes montre que les calmars des eaux tempérées complètent leur cycle vital en moins de 2 ans alors que les espèces tropicales vivent moins de 8 mois. L'estimation de l'âge des individus a également facilité l'identification des cohortes par l'analyse des distributions des dates d'éclosion. L'analyse grandeur–âge a été appliquée dans des études préliminaires de modélisation de la croissance et il existe une demande continue pour des modèles plus précis de la croissance des calmars fondée sur l'âge. Il est donc possible de recourir à des systèmes d'analyse d'images pour dénombrer les accroissements et analyser leur largeur. Les études subséquentes devraient viser à obtenir de l'information sur l'âge d'un plus grand nombre d'espèces, en tenant compte de la manière dont d'autres caractéristiques de la microstructure des statolithes, comme les zones, pourraient refléter les habitats antérieurs et en déterminant comment la longueur ou le poids des statolithes pourraient être liés aux antécédents de croissance.

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The study of the growth, longevity, and life history of squids has been plagued with uncertainties and difficulties. It is, therefore, the purpose of this paper to examine and synthesise research results concerning the use of statolith increments for determining the age and growth rates of squids and sepioids. Rapid growth in individual squids, along with the migrations undertaken by some species, has made the more traditional length–frequency analysis used for fin-fish difficult, if not impossible, to interpret when used on cephalopods. At least five different growth models have been applied to one family of squids (the Loliginidae; Hixon 1980; Mangold 1983), creating considerable confusion. Early last decade, Voss (1983) commented that "the biology of no species of cephalopod is as well known as that of almost any commercially exploited fin fish." Fortunately, this situation is gradually changing and a better understanding of the age and life histories of squids is developing.

The search for a method to measure the age of squids has encompassed analyses of periodic laminae in beaks, radulae, gladii, and statoliths (Rodhouse and Hatfield 1990a). Of these structure the statoliths have proven to be the most promising for age and growth studies (see Jereb et al. 1991). Recently, however, increments along the gladius are also showing potential as an ageing tool (see Koronkiewicz 1990; Arkhipkin and Bizikov 1991; Bizikov 1991; Jackson et al.

1993). Considerable information has been amassed on the validation of statolith increment periodicity and the relationship between squid size and age. Work is now beginning to focus on the use of size-at-age information for the construction of squid growth models, and the identification of individual cohorts through analysis of hatch date distributions. However, there is much more information that can yet be obtained from statolith increment analysis.

Culturing squids throughout their life cycle has also facilitated the corroboration of results from statolith ageing studies. Improvements in culturing technology have provided a further means to increase knowledge of squid growth and population dynamics over the last decade (e.g., Hanlon and Hixon 1983; Hanlon et al. 1983; Yang et al. 1983, 1986; Forsythe and Van Heukelem 1987; Forsythe and Hanlon 1989; Hanlon et al. 1987, 1989; Hanlon 1987, 1990; Jackson et al. 1993).

The Statolith

Squids and sepioids possess a pair of calcareous statoliths each of which is attached to the anterior wall of their statocyst chambers. The paired statocyst chambers lie at the back of the cephalic cartilage. The morphology and the neurobiological function of the squid statolith–statocyst system has been studied extensively (Dilly 1976; Morris and Aldrich 1984; Young 1989; Budelmann 1988) and has been considered to be an analogous system to the vertebrate semicircular canal system (Stephens and Young 1978; Williamson 1989a, 1989b). The teuthoid and sepioid statolith is generally composed of four parts (Fig. 1): dorsal dome, lateral dome, rostrum, and wing (although there is substantial diversity in shape), and is considerably different from the statolith of octopods (see Clarke 1978; Arkhipkin and Murzov 1986a; Rodhouse and Hatfield 1990a; Lipinski et al. 1991). The teuthoid statolith is predominantly translucent except for the wing, which is opaque and composed of loosely packed crystals. The wing is where the statolith is attached to the statocyst wall via a structure referred to as the macula princeps (Dilly 1976; Rodhouse and Hatfield 1990a). The statoliths of *Nautilus* spp. are completely different from the paired statoliths of all other cephalopods. The paired statocysts of *Nautilus* spp. each have numerous small (1.7–17.2 μm) ovoid statoliths that half fill the statocyst cavity (Morris 1989).

Growth increments (Fig. 2) have been found within the statoliths of many species of squid and in the statoliths of several species of sepioids. However, there has been some variability with regard to the terminology of the periodic layers observed within the squid statolith microstructure. "Ring" has been a common descriptor in the past but problems with this descriptor lie in the fact that any single "ring" is a three dimensional structure (S.E. Campana, personal communication). Lipinski et al. (1991) have provided some guidance with regard to future terms for microstructural features of statoliths. They have not advocated use of the term "growth ring" but have suggested that "dark ring" and "light ring" refer to what is observed under the microscope, and that a 'dark ring' and an adjaent 'light ring' together make up an "increment." For squid and sepioid species, 'increment' refers to the paired dark and light growth layers produced over a 24-h period. I will adopt the current convention and use increment to refer to the bipartite structure

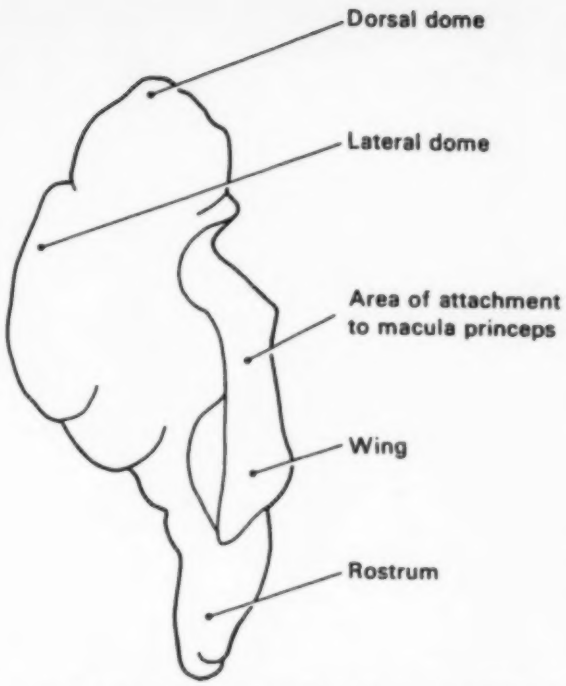

FIG. 1. Generalised teuthoid statolith (right statolith, anterior view) showing prominent microtopographical features referred to in the text (from Rodhouse and Hatfield 1990a).

within the statolith composed of both a dark and a light ring. Increment is now also commonly used for analogous structures observed in fish otoliths (see Stevenson and Campana 1992).

Pannella (1971) was the first to show that visually discernible growth layers within the otolith microstructure of fish represent daily growth increments. Since 1971, there has been a dramatic increase in the use of daily otolith increments to study the life history and demography of fish (for reviews see Campana and Neilson 1985; Jones 1986; Stevenson and Campana 1992). Much of the research now being carried out on squid statoliths parallels that on fish otoliths, as the squid statolith microstructure is composed of increments that are very similar in appearance to daily increments in fish otoliths (Arkhipkin 1988).

Young (1960, cited in Dawe and Natsukari 1991) was the first to note the presence of periodic increments within the statoliths of the myopsid squid *Alloteuthis subulata*. Clarke (1966) also noted the presence of increments within the ommastrephids *Ommastrephes caroli*, *O. pteropus*, and *Todarodes sagittatus*. However, it was 12 yr before anyone attempted to analyse these increments as tools for ageing, with the initial work carried out on *Illex illecebrosus* (Lipinski 1978, 1979, 1980a, 1980b) and *Loligo opalescens* (Spratt 1978, 1979). Research into statolith growth increments may have been hindered by the conclusions of Dilly (1976), who found no evidence of growth rings in the statoliths he analysed and suggested that "any diurnal rhythm is probably too rapid to affect the statoconial crystal growth."

It is still not clear what mechanisms govern the production of increments within the statolith microstructure. Morris

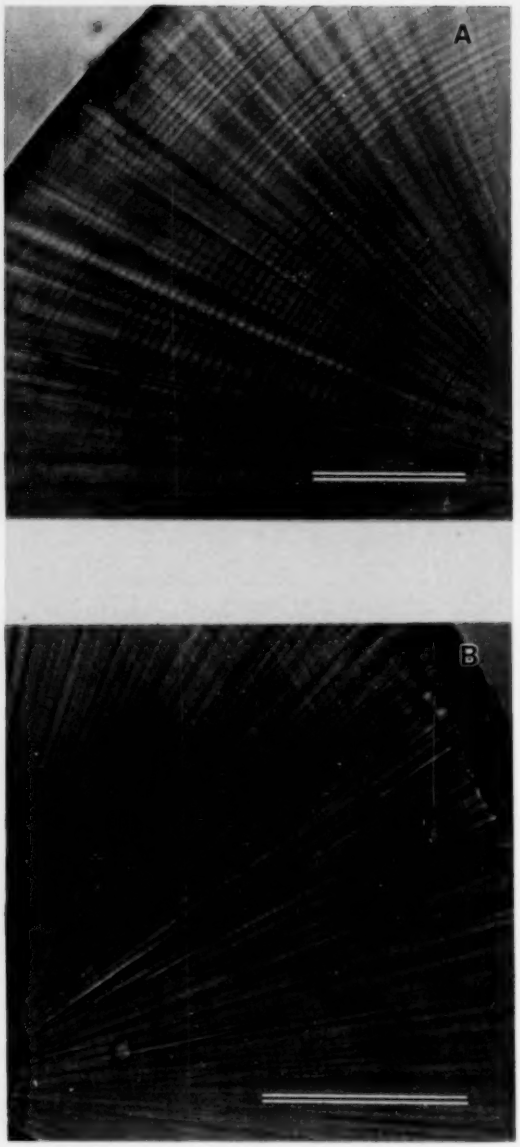

FIG. 2. Examples of daily statolith growth increments from two tropical loliginid squids. (A) whole statolith of *Loliolus noctiluca* (female, 59 days, 52 mm mantle length) mounted in the thermoplastic cement Crystal Bond. Scale bar = 50 μm. (B) Statolith of *Loligo chinensis* which has been ground and polished on both the anterior and posterior surfaces to produce a thin section (male, 78 days, 110 mm mantle length). Scale bar = 100 μm. (From Jackson 1990b)

(1991a) proposed an initial theory involving pH changes in the statocyst fluid; these changes were seen to either promote or inhibit calcification based on amino acid metabolism and squid activity levels. Recently, Lipinski (1993) has provided a more detailed hypothesis and suggested that periodic changes (possibly related to squid activity levels) in strontium concentrations in the statocyst fluid are probably more important than pH changes in cyclical calcification leading to growth increment production. Lipinski (1993) suggested that after hatching, diel activity patterns may result from a genetically controlled but environmentally induced circadian rhythm, even in squids living in a stable environment.

Increment Patterns and Taxonomic Groups

Most studies have documented statolith increments in the myopsid and oegopsid squids. Increments have also been identified in several sepioids, with daily increments demonstrated in *Idiosepius pygmaeus* (Jackson 1986, 1989). Increments have also been recorded in the sepioid *Rossia glaucopis* (Kristensen 1980). Recently, Raya et al. (1992) documented increments within the statolith of the sepioid *Sepia hierredda* off the northwest African coast. However, the low number of increments observed in *S. hierredda* suggests that increments are not produced daily. Octopus statoliths are very different in shape and crystal structure to statoliths of squids and sepioids (Clarke 1978; Tait 1980). Moreover, statolith increments like those observed for squids have not been observed for any octopus species. Based on current techniques, it is therefore unlikely that octopus statoliths will be useful structures for research into ageing.

Methods of Preparing Statoliths for Increment Analysis

Numerous techniques have been developed for the visualisation of statolith increments under light microscopy. Statoliths of small species (e.g., *Idiosepius pygmaeus*) or paralarvae can often be mounted whole and increments observed in a histological mounting medium such as DPX (dibutyl–phthalate–polystyrene–xylene) or even in a thermoplastic cement such as Crystal Bond (see Jackson 1990a; Jackson and Choat 1992). However, statoliths of larger species often require grinding and polishing to reveal the increments.

There is considerable variation in the readability of statolith increments between species (e.g., Lipinski 1981; Jackson and Lu 1994). The readability of statolith increments varies not only with size but also with species. For example, statoliths of the loliginid *Loliolus noctiluca* are extremely clear and can be observed in whole statoliths mounted in the thermoplastic cement Crystal Bond (Jackson 1990b). However, similar-sized statoliths from *Loligo chinensis*[1] (which has a distribution that overlaps with *L. noctiluca*) normally require grinding and polishing to reveal the increments.

Techniques for statolith extraction and preparation for light microscopy are numerous and have been described in many of the publications dealing with cephalopod age and growth (e.g., Spratt 1978, 1979; Lipinski 1980a, 1980b; Dawe et al. 1985; Hurley et al. 1985; Jackson 1989, 1993b). Several summaries deal with the techniques needed for statolith extraction and increment resolution (Lipinski 1981; Arkhipkin and Murzov 1985; Rodhouse and Hatfield 1990a; Arkhipkin 1991; Lipinski et al. 1991; Dawe and Natsukari 1991). A useful summary of statolith preparation and increment counting

[1] *Loligo chinensis* in Australia is now known to be a new species which is currently unnamed (J. Yeatman, James Cook University, Townsville, personal communication). Furthermore all *Loligo* in Australia will probably be referred to as *Photololigo* in the future. As considerable ageing work has been carried out on *L. chinensis* in Australia, I have referred to this species by the old name to avoid confusion.

TABLE 1. Summary of studies validating increment periodicity in cephalopod statoliths.

Species	No. of individuals	Technique	Reference(s)
		Sepioidea	
Idiosepius pygmaeus	6	Tetracycline, ambient exposure	Jackson 1989
		Teuthoidea (Myopsida)	
Alloteuthis subulata	11	Tetracycline injection	Lipinski 1986
Loligo opalescens	29	Comparing known age to increment count	Hixon and Villoch 1984; Yang et al. 1986
Loligo chinensis	2	Tetracycline injection	Jackson 1990b
Loliolus noctiluca	9	Tetracycline, ambient exposure	Jackson 1990b
Sepioteuthis lessoniana	7	Tetracycline, calcein, ambient exposure	Jackson 1990a
Sepioteuthis lessoniana	36	Comparing known age to increment count	Jackson et al. 1993
		Teuthoidea (Oegopsida)	
Illex illecebrosus	40	Comparing increment number to elapsed days between 2 cohorts	Hurley et al. 1979
Illex illecebrosus	4	Strontium given with food	Hurley et al. 1985
Illex illecebrosus	8	Strontium, tetracycline given with food/force fed	Dawe et al. 1985
Illex argentinus	100	Comparing increment number to elapsed days in successive field samples	Uozumi and Shiba 1993
Todarodes pacificus	4	Tetracycline given with food	Nakamura and Sakurai 1990
Todarodes pacificus	17	Tetracycline given with food	Nakamura and Sakurai 1991
Nototodarus sloanii	97	Comparing increment number to elapsed days in successive field samples	Uozumi and Ohara 1993
Abralia trigonura (paralarvae)	15	Comparing known age to increment count	Bigelow 1992
Onychoteuthis borealijaponica	3	Tetracycline, ambient exposure	Bigelow 1994

techniques for light microscopy has been provided in Dawe and Natsukari (1991), and Lipinski (1991) has provided a summary of techniques for statolith preparation for scanning electron microscopy (SEM).

Evidence for Daily Periodicity in Increment Formation

Unlike fish otolith studies, in which considerable work has focused on the validation of the daily periodicity of otolith increments, validation studies of squid and sepioid statolith increments have not been as extensive. This is because fewer researchers are working on cephalopods, and because considerable difficulties are encountered with obtaining live squids and maintaining them in captivity. Information on statolith increment periodicity (Table 1) has been achieved (i) indirectly, by comparing the number of increments in a subsample of squid by following the same mode in successive length–frequency samples, (ii) directly, by culturing squids of known age and comparing increment number with squid age, and (iii) directly, by placing a chemical mark on the statolith and then comparing the number of elapsed days with the number of increments produced since the time of marking.

(i) Indirect Methods

Several studies have attempted to obtain statolith age estimates of a common group that is sampled at different periods. By comparing the mean group (or modal) age over successive periods, it is possible to compare the number of increments with the number of elapsed days between samples. For example, Hurley et al. (1979) found that the difference in the mean cohort age of a subsample of two successive cohorts of *Illex illecebrosus* underestimated the time (in days) between the two modes. However, the time difference in this study fell just within the 95% confidence limits of the difference in the mean cohort age between the two subsamples (see also Dawe 1981). Obtaining statolith-derived ages of individual squids in successive group modes has been used with two other ommastrephids, *I. argentinus* (six successive samples) on the edge of the Patagonian Shelf (Uozumi and Shiba 1993) and *Nototodarus sloanii* (five successive samples) off southern New Zealand (Uozumi and Ohara 1993). In both of these studies, successive samples were taken over short periods of time in restricted areas. The resulting regressions (of sampling date vs. mean modal squid age) supported a daily periodicity in increment production.

Employing such an indirect method to attempt to obtain information on increment periodicity, however, remains questionable because of a number of biases in such an analysis. Identifying a common group in successive samples for length frequency analysis can be difficult (Caddy 1991, see also Hatfield 1991a; Hatfield and Rodhouse 1994). Furthermore, any group of squid that is subjected to successive sampling is not exempt from effects of migration (e.g., see Arkhipkin 1993a), size dependent mortality, or sampling gear selectivity.

(ii) Culture

Some evidence is available for daily statolith increment periodicity from squids raised in culture. A positive relationship (in support of daily periodicity) was obtained between increment number and actual age for cultured paralarvae of

Abralia trigonura (Bigelow 1992), juveniles of *Loligo opalescens* (Hixon and Villoch 1984; Yang et al. 1986), and for *Sepioteuthis lessoniana* raised throughout its life cycle (Jackson et al. 1993). Although these experiments give support to daily-increment periodicity, Jackson et al. (1993) have discussed the high probability of accepting a type II error (i.e., failing to reject a false null hypothesis) from such experiments with limited data sets.

Some squid species lay down numerous increments within the statolith during embryonic development. However, it is likely that embryonic increments are not produced daily. Culture experiments with embryos of *Alloteuthis subulata* by Morris (1991b) found that the increments in this species are not laid down daily during embryonic development and that increment number was more related to statolith size than to individual age (see also Rodhouse 1991a).

A more convincing argument in support of daily periodicity in statolith increment production is in the comparison of squid of known-age (i.e., individuals whose ages are known because they were raised from hatching) to age estimates obtained from statolith-aged field specimens. Statolith age estimates of adult individuals of *L. opalescens* captured off California (Jackson 1991a, 1994) agreed with age data for this species raised in captivity by Yang et al. (1986). Although wild individuals appeared to be somewhat faster growing than the cultured squids, there was some overlap in the length-at-age data from both studies. There was also strong agreement in the form of growth when comparing known size-at-age data from *S. lessoniana* raised in captivity with statolith-derived size-at-age data for specimens captured off northern Australia (see Jackson et al. 1993). Even though utilising statolith ageing techniques in conjunction with squid culture experiments has been preliminary in nature, the combining of these two methods promises to be a useful technique for validating increment periodicity at all stages of the life cycle.

(iii) Validation by Chemical Marking

Marking statoliths with an in situ chemical mark and maintaining squids alive under experimental conditions has been a successful, direct means of establishing the periodicity of statolith growth increments. Various forms of tetracycline have been the most common chemical used (either injected or dissolved in seawater for ambient exposure). However, calcein and strontium have also been used successfully for producing a fluorescent mark on the statolith (see Table 1). All experiments undertaken to date provide strong support that increments are produced on a daily basis. Because of the difficulty associated with maintaining squids in captivity, it has been difficult to obtain large sample sizes. However, results from one sepioid, four myopsid squid, and four oegopsid squid (Table 1) all support the daily periodicity in increment formation. There is clearly the need to continue validation work to further explore statolith increment periodicity. Work needs to be focused on validating increments at all stages of the life cycle, especially near maximum size to document increment periodicity in very large individuals.

Application of Increment Data to Biological Studies

Fish Larval Studies

The ability to age field-captured squids provides an opportunity to undertake a number of biological studies that would be otherwise impossible. Many of the techniques used in larval fish otolith studies published since Pannella's (1971) original description of daily otolith increments (e.g., Campana and Neilson 1985; Jones 1986; Stevenson and Campana 1992) could be applied to squid statolith analysis to obtain powerful ecological information. For example, direct application of size-at-age information has been successfully used to identify growth variation in fish larvae from different geographical areas (e.g., Brown and Bailey 1992; Ré and Goncalves 1993). However, otolith increment width analysis is also a method of providing time-specific information on growth rates. Victor (1982) initially noted that increased feeding was reflected in wider otolith increments. Research is now being focused on using otolith increment width data for determining growth efficiencies of larval fish. For example, Moksness and Fossum (1991) have been able to identify spring and summer spawned North Sea herring by analysing increment widths, while Moksness (1992) was able to use increment widths to also identify North Sea herring from different geographical areas. Maillet and Checkley (1991) found a relationship between storm events and increment widths in larval Atlantic menhaden. Storm events were shown to result in decreased otolith increment widths owing to decreased growth rates resulting from dispersion of food organisms.

The above examples reveal that fish larvae do have the ability to rapidly record environmental responses in their otolith increment width sequence. However, in a recent review Jones (1992) commented on how incremental growth in fish otoliths responded differently to environmental changes based on age of the fish and physiological tolerance. For example, juvenile fish often integrate their growth response to temperature change over several days whereas larvae experience an immediate change in growth rate. Hence, sudden changes in increment widths may be easier to relate to ambient environmental information for larvae rather than for juveniles.

It is, therefore, important that squid statolith workers not ignore the techniques being developed by larval fish otolith workers. An obvious advantage of squid statoliths is that increments are laid down throughout their short life cycle (see Jackson 1990a; Jackson and Choat 1992; Jackson et al. 1993), which means that daily responses to changes in growth rates can be monitored over an extended period. Moreover, both squids and larval fish exhibit exponential growth. Because of the rapid growth of squid, they should respond quickly to environmental changes (e.g., changes in food supply or ambient temperature) rather than to integrate such changes over several days.

Information Revealed from Statolith Increments

(i) Age

Perhaps the most outstanding contribution that ageing studies have made to cephalopod biology was the (initially surprising) discovery that squids are generally much shorter lived than was commonly thought (see also Hiller 1990). This information contradicted results from length–frequency analysis, which indicated a long lifespan and slow growth (see Jackson and Choat 1992). The early hesitation to accept the interpretation of daily production of statolith increments was probably due to researchers not accepting that squids could possibly be that young! For example, Spratt (1978, 1979) suggested that increments near the nucleus in

L. opalescens statoliths were probably daily but that more prominent increments in the rostrum were possibly monthly in periodicity, suggesting at least a 2-yr lifespan. However, later research (e.g., Yang 1986; Jackson 1991a, 1994) favoured daily periodicity.

To gain an overview of the lifespan of squids, literature on size-at-age was reviewed (Table 2). From these papers, the oldest individual was included in the table. In many instances this was not the largest individual because of the great variation in size-at-age in many species. For some of the papers, age was obtained from only one (e.g., Jackson et al. 1991; Lipinski 1991; Gauldie et al. 1994) or several individuals (e.g., Martins 1982; Rodhouse 1991b).

The maximum recorded age (Table 2, based on the assumption of daily periodicity of increments in all studies) ranges from the small sepioid *Idiosepius pygmaeus* (72 d, <20 mm ML) (Jackson and Choat 1992) to the North Pacific Gonatid *Berryteuthis magister*, which is reported to be over 1400 d (>200 mm ML) (Natsukari et al. 1993). Except for *B. magister*, and *Todaropsis eblanae* (Lipinski et al. 1993) all the species for which statolith age estimates are available are under 2 yr, with the majority of temperate species at around 1 yr and tropical species (*Idiosepius pygmaeus*, *Loliolus noctiluca*, *Loligo chinensis*, *Sepioteuthis lessoniana*, *Alloteuthis africana*, *A. subulata*, and *Enoploteuthis leptura*) less than 8 mo.

The table below summarizes conflicting age results that have arisen for statolith age studies for some squid species:

Species	Age (d)	Mantle length	Reference
Todarodes angolensis	384	~403	Villanueva 1992
	648	~259	Lipinski et al. 1993
Todarodes eblanae	~310	162	Lipinski 1991
	210	140	Arkhipkin 1989
	787	~153	Lipinski et al. 1993
Gonatus fabricii	~320	~190	Wiborg et al. 1982b
	~609	~172	Kristensen 1980
Berryteuthis magister	268	233	Bizikov 1990
	~1470	~233	Natsukari et al. 1993

These differences emphasise the need for further research on these species, and suggest that the increment sequences within the statoliths of some species may be ambiguous. It is thus uncertain whether any species of squid studied thus far lives longer than 2 yr. For *G. fabricii* the age estimates by Kristensen (1980) are possibly inflated because he identified some more prominent increments as being formed fortnightly.

Because age estimates of squid are so different among these studies, there may be patterns other than daily increments (e.g., subdaily increments) within the statolith microstructure. Such discrepancies have been noted by Lipinski and Durholtz (1994), who have emphasised the need for rigorous statolith analysis for such species. These discrepancies reveal the considerable amount of subjectivity that is involved in identifying a daily increment in some species. Validation experiments are one means that would discriminate between daily and subdaily increments in such species. Such problems are also encountered in fish otolith studies as inflated age estimates can result from mistaking subdaily increments for daily increments. This has been well addressed by Campana (1992). Campana (1992) has demonstrated how over grinding an otolith of starry flounder (*Platichthys stellatus*) can make subdaily increments more prominent than the daily increments within the otolith microstructure. In Fig. 8 of Campana (1992) approximately 55 subdaily increments could be counted in a 12 d sequence of daily increments on a light micrograph. Such a problem may account for the widely different counts obtained in *Todarodes* and *Berryteuthis magister* statoliths cited above. There is thus the need to identify the difference between subdaily and daily increments for such species (see Okutani et al. 1993, p. 682, comments by Jackson and Nesis). In contrast, maximum ages of other ommastrephids from different studies (e.g., *Illex illecebrosus*, *I. argentinus*, and *Todarodes sagittatus*, Table 2) are more similar, indicating that the increment sequences are probably easier to discern (or at least less ambiguous) than some of the species discussed above.

Statolith age estimates can also provide a useful means for obtaining age-specific information on growth and maturation processes. Jackson (1991a, 1993a) was able to follow growth of the gonad with age for both male and female individuals of *L. chinensis* and *I. pygmaeus* and was thereby able to discern seasonally induced differences in gonad growth and age at reproduction in both of these species. These trends were completely masked without a knowledge of individual age. Further studies should reveal the degree of plasticity in maturation rates and gonad growth in other species.

(ii) Growth modelling

Because statolith increments can provide an estimate of individual age, these estimates can provide information on the form of growth when graphed as a scatterplot of size-at-age for a number of individuals (preferably captured at a similar time and locality). Such scatterplots can be used for regression analyses; data sets from different times or localities can further be compared by analysis of co-variance (e.g., Jackson and Choat 1992). Linear regression analysis can often be used to model growth over a restricted phase of the life-span (e.g., Jackson and Choat 1992; Dawe and Beck 1992; Rodhouse and Hatfield 1990b). For more complete data sets, curvilinear growth models can be developed to describe growth over a greater proportion of the lifespan (e.g., Hatfield 1991b; Macy 1992; Villanueva 1992).

Only a few studies (Natsukari et al. 1988; Kinoshita 1989; Uozumi and Shiba 1993; Uozumi and Ohara 1993) have modelled squid growth using asymptotic models. However, Alford and Jackson (1993) have discussed possible reasons for how nonasymptotic size-at-age data might be analysed to produce an asymptotic curve. In contrast, most studies have attempted to model growth using nonasymptotic growth models (Fig. 3), including linear, exponential, double exponential, and power curves (see Table 2).

A peculiar feature of some scatterplots of size-at-age appears to be the difficulty in fitting a single model to the scatterplot. For example, Jackson (1991a) and Bigelow (1992) have modelled growth based on an exponential phase followed by a linear phase. Furthermore, some length-at-age scatterplots (e.g., *Nototodarus sloanii*, Uozumi and Ohara 1993, Fig. 7; *Todarodes angolensis*, Villanueva 1992,

TABLE 2. Summary of maximum age and growth models determined from statolith ageing ("~" indicates approximate value extracted from data given in paper, "*" indicates gladius length not ML, M indicates males). The mantle length corresponds to the oldest individual reported.

Species	Age (d)	Maximum ML (mm)	Growth model	Reference
		Sepioidea		
Idiosepius pygmaeus	72	12.8	Linear	Jackson and Choat 1992
		Teuthoidea (Myopsida)		
Loliolus noctiluca	112	90		Jackson and Choat 1992
Loligo chinensis	173 (winter)	167	Linear (juveniles + adults)	Jackson and Choat 1992
Loligo chinensis	115 (summer)	167	Exponential (whole size range)	Jackson 1991a
Photololigo edulis	350	~404	Logistic	Natsukari et al. 1988
Photololigo edulis			Exponential	Alford and Jackson 1993
Heterololigo bleekeri	385.5	320	Logistic	Kinoshita 1989
Loligo gahi	439 (season 1, M)	~115	Log-linear	Hatfield 1991b
Loligo gahi	~388 (season 2, M)	~380	Log-linear	Hatfield 1991b
Loligo gahi	396	~268		Arkhipkin 1993b
Loligo pealei	256	406	Logarithmic	Macy 1992
Loligo vulgaris	~245	~274	Double exponential	Natsukari and Komine 1992
Loligo vulgaris reynaudii	~540	~360		Lipinski 1991
Loligo vulgaris reynaudii	~470	~411		Lipinski and Durholtz 1994
Loligo forbesi	450	740		Martins 1982
Sepioteuthis lessoniana			Exponential + linear (males + juveniles only)	Jackson 1991a
Sepioteuthis lessoniana	188	184		Jackson 1990a
Alloteuthis africana	208	205		Arkhipkin and Nekludova (1993)
Alloteuthis subulata	231	135		Arkhipkin and Nekludova (1993)
		Teuthoidea (Oegopsida)		
Illex illecebrosus	~214	~256	Linear	Radtke 1983
Illex illecebrosus	~233	~245	Linear	Morris and Aldrich 1985
Illex illecebrosus	210	217		Arkhipkin 1989
Illex illecebrosus	<180	<250	Exponential	Hurley and Beck 1979
Illex illecebrosus	~247	~282	Linear	Dawe and Beck 1992
Illex argentinus	380	270		Arkhipkin 1990
Illex argentinus	~378	~327	Linear	Rodhouse and Hatfield 1990b
Illex argentinus	366	~241	Logistic/linear	Uozumi and Shiba 1993
Illex argentinus	~338	~315		Arkhipkin 1993a
Illex coindetii	270	290		Arkhipkin 1989
Todarodes sagittatus	421	~514	Linear	Rosenberg et al. 1981
Todarodes sagittatus	432	500		Wiborg and Gjosaeter 1981
Todarodes sagittatus	~434	~488	Linear	Wiborg et al. 1982a
Todarodes sagittatus	340	500		Shimko 1984
Todarodes angolensis	384	~403	Power	Villanueva 1992
Todarodes angolensis	648	~259	Linear	Lipinski et al. 1993
Todarodes filippovae	285	340		Arkhipkin 1989
Todaropsis eblanae	787	~153	Linear	Lipinski et al. 1993
Todaropsis eblanae	210	140		Arkhipkin 1989
Todaropsis eblanae	~310	162		Lipinski 1991
Nototodarus sloanii	318	386	Logistic	Uozumi and Ohara 1993
Sthenoteuthis oualaniensis	397	565	? logistic, not stated	Arkhipkin and Bizikov 1991
Stenoteuthis pteropus	372	422	? exponential, not stated	Arkhipkin and Mikheev 1992
Dosidicus gigas	~274	~490		Arkhipkin and Murzov 1986b
Dosidicus gigas	355	720		Arkhipkin 1990
Martialia hyadesi	327	315		Arkhipkin 1989
Ornithoteuthis antillarum	195	138		Arkhipkin 1989
Martialia hyadesi	367	233		Rodhouse 1991b
Gonatus fabricii	~609[a]	~172*	Linear	Kristensen 1980
Gonatus fabricii	~320	~190		Wiborg et al. 1982b
Berryteuthis magister	~1470	~233	Double exponential	Natsukari et al. 1993
Berryteuthis magister	268	233		Bizikov 1990

TABLE 2. (*Concluded*)

Species	Age (d)	Maximum ML (mm)	Growth model	Reference(s)
Abraliopsis atlantica	142	33	Logarithmic	Arkhipkin and Murzov 1987
Abralia trigonura	130	~32	Exponential + ?linear	Bigelow 1992
Enoploteuthis leptura	153	72		Arkhipkin 1994
Moroteuthis ingens	350	340	Linear	Arkhipkin and Bizikov 1991
Moroteuthis ingens	351	440	Linear	Jackson 1993b
Onychoteuthis borealijaponica	394	245	Exponential/logistic	Bigelow 1994
Architeuthis sp.	153	422		Jackson et al. 1991
Architeuthis kirki	393	1610		Gauldie et al. 1994

[a]Using fortnightly rings.

Fig. 7 and 8) appear difficult to model with a single equation. Because squids display a great degree of plasticity in individual growth rates, this inevitably leads to much variation in a size-at-age plot (e.g., Wiborg et al. 1982a; Hatfield 1991b; Arkhipkin 1993a). Fitting a single growth model is difficult because individual growth histories vary considerably. In several studies (Rodhouse and Hatfield 1990b; Dawe and Beck 1992) growth modelling has been facilitated by selecting individuals from restricted periods of hatching (thereby reducing variability in size-at-age).

The rapid growth displayed by many cephalopods makes them sensitive to changes in environmental temperatures (Forsythe 1993). Thus, squids sampled at different times of the year can have very different growth parameters and/or maximum ages (Natsukari et al. 1988; Jackson 1991a, 1991b; Jackson and Choat 1992; Dawe and Beck 1992; Arkhipkin 1993a). Such considerations need to be taken into account when attempting growth modelling.

The results to date suggest that squids and some sepioids have a form of growth that is very different from the generalised von Bertalanffy growth curve used in fin fish modelling, despite past attempts to model squid growth using asymptotic models (Pauly 1985; Jarre et al. 1991). Furthermore, the juvenile phase of growth can be quite extended. Thus, some species of squids may actually spend only a short period of their life-span as large individuals (e.g., *Loligo chinensis*, Fig. 3D).

There is a need to develop a more comprehensive model for squid growth (see Bello 1991; Ragonese et al. 1991). The fact that size-at-age data indicate nonasymptotic growth suggests that fin fish models are not applicable for squids. Alford and Jackson (1993) have identified potential pitfalls in the modelling of squid growth and have shown that size-at-age data should not be reduced to means, but that the whole data set should be used when growth is modelled to avoid potential asymptotic artefacts. Alford and Jackson (1993) also suggested that the null hypothesis for a growth model should be a nonasymptotic model. Because the exponential model is the simplest, it has been recommended as the model to be evaluated first. Statolith age and growth analysis has expanded to the point where there is a need for a consensus with regard to growth modelling. I suggest that future researchers carefully consider the form of growth in squids and that effort be focused on the selection and evaluation of nonasymptotic growth models. It is necessary that researchers clearly state the model used in curve fitting (as this has been overlooked in some studies) and it would be advantageous to record the results of any other attempts at fitting curves to their data.

(iii) Cohort analysis – hatching dates

Age estimates of individuals are useful for identifying cohorts and for determining seasonality in reproduction by back-calculating hatching dates. This is especially important in squids because of the considerable variability in size and maturity displayed in individuals of similar age. Hatch-date analysis has generally revealed that hatching often occurs over an extended period but that there is often a peak in hatching.

For loliginids, Natsukari et al. (1988) was able to divide his growth analysis of *Loligo edulis* into two cohorts (a warm and cold season brood) by analysing time of hatching. Similarly, Hatfield (1991b) also identified two spawning groups of *L. gahi* in the South Atlantic, those that hatched between May and February, with a peak in mid-August (austral winter) and those that hatched between September and March with a peak in December (austral summer). In contrast, Natsukari and Komine (1992) identified only one major peak in hatching for *L. vulgaris* with 70% of the specimens analysed having hatched between mid-May to early July and all individuals hatched between March and September, while Arkhipkin and Nekludova (1993) identified a restricted hatching period for the tropical loliginids, *Alloteuthis africana* and *A. subulata* (sampled in August–September), between January and July with peaks in March–May. Also, *Loligo pealei* off Rhode Island, which hatched between July and January, showed a single major peak in October–November (Macy 1992).

Hatch-date distributions derived from statoliths have also been determined for some ommastrephids. While hatching occurs at various times, statolith analysis has revealed that it is not uncommon for hatching to take place over winter. Rodhouse and Hatfield (1990b) found that *Illex argentinus* on the Patagonian Shelf hatches throughout the austral winter, peaking in June–July. These results were corroborated by Uozumi and Shiba (1993) who identified a major spawning peak from May–July but also identified a second spawning peak in the austral summer (December–February). Further north off the Argentinian Shelf, Arkhipkin (1990) identified four cohorts of *I. argentinus* that spawned each season. *Illex illecebrosus* in the Northwest Atlantic was found to have predominantly a spring peak in hatching (from March to May) but with some hatching occurring from December to June (Dawe and Beck 1992). In the Northeast Atlantic, Wiborg et al. (1982a) found that although *T. sagittatus* had an extended spawning season, it also had a spring peak, with a second peak in autumn–winter. Wiborg and Beck (1984) also identified a winter peak in hatching for this species. *Todarodes pacificus* in northern Japanese waters was also found to hatch predominantly in autumn–winter

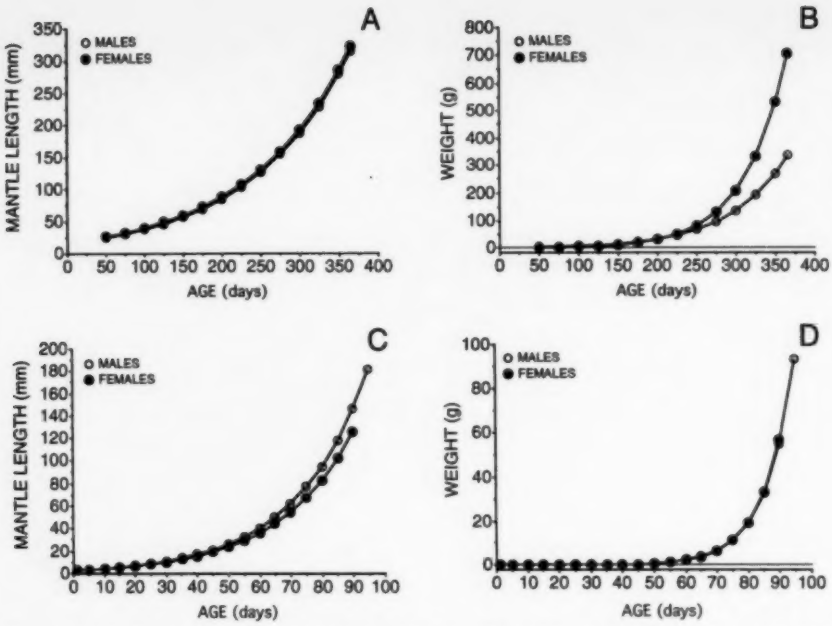

FIG. 3. Examples of nonasymptotic exponential growth models (for both mantle length and weight) that have been developed for two species of squid. (A, B) Growth models for males and females of the subarctic North Pacific onychoteuthid squid *Onychoteuthis borealijaponica* (from data given in Bigelow 1994). (C, D) Growth models for the tropical Australian loliginid squid *Loligo chinensis* (summer population) (from Jackson 1991a). Note how based on weight (Fig. 3D), *L. chinensis* spends up to 80% of its lifespan as a small individual less than 20 g.

with some hatching taking place in early spring (Nakamura and Sakurai 1993), while *Nototodarus sloanii* off southern New Zealand was found to hatch predominantly in winter, although some hatching appeared to take place year round (Uozumi and Ohara 1993). Similarly Rodhouse et al. (1994) found that *Martialia hyadesi* hatched in winter in the Antarctic Polar Frontal Zone, whereas individuals from the Patagonian Shelf Edge hatched in spring.

In other oegopsid species, Natsukari et al. (1993) found hatch-date distributions to differ for *Berryteuthis magister* at two different localities (Japan Sea and Okhotsk Sea). This species was found to spawn in all months of the year but the Japan Sea population was found to peak in June, while there was no pronounced seasonality in hatching in the Okhotsk sea population. Wiborg et al. (1982b) identified a hatching period for *Gonatus fabricii* in the Barents Sea from November to May with a peak in March. Bigelow (1994) found that *Onychoteuthis borealijaponica* in the North Pacific hatched in all months except March.

Perhaps the most interesting and useful application of statolith age analysis has been carried out in a detailed study by Arkhipkin (1993a) who employed statolith analysis for a detailed cohort and migration analysis of *Illex argentinus* off Argentina. By ageing individual squids, Arkhipkin (1993a) was able to put a time scale on the migration of this species from 52° to 46°S and analyse growth of squids over this migration. This study also revealed that analysis of length–frequency data from successive samples taken at a similar locality could not be used for growth analysis as each successive sample would represent a different cohort of squid moving through the locality. Detailed statolith analysis also revealed a different microstructure among squids owing to locality differences. Arkhipkin (1993a) found that the increments laid down during the jvuenile phase of growth were very different depending on the growth history of the individual. Juveniles that hatched in winter in the cold waters of the Argentine basin had well distinguished narrow (2–3 μm) increments. In contrast, juveniles that hatched in the winter but fed in warm waters of the Patagonian Shelf had a faster growth rate that was reflected in wider (4–5 μm) less well defined increments (see also Arkhipkin and Scherbich 1991).

Other Applications of Statolith Increment Analysis and Future Research

A review of the literature has revealed that statolith increment analysis started with the documentation of the increments and early analysis of possible ages of squids, which led to the construction of size-at-age scatterplots and the subsequent (somewhat preliminary) modelling of growth. Concurrent with this research have been validation studies that have given support to daily-increment periodicity. Apart from obtaining size-at-age information, it may also be possible to obtain ecological information on the past history of some species of oceanic squids. Jackson (1993b) commented on two very distinct regions within the statolith microstructure of the deepwater squid *Moroteuthis ingens* off New Zealand. The statolith microstructure consisted of two very well defined zones (an inner opaque zone followed by an outer translucent zone). Very fine increments (resembling

daily increments in other species) were present in both of these zones. These two zones were found to resemble zones found in some fish otoliths, which were known to be related to a habitat shift during the fish's life history. Because *M. ingens* is a demersal species, Jackson (1993b) proposed a hypothesis that these two zones reflect a habitat shift from a pelagic (opaque zone) to a demersal (translucent zone) phase of growth. More recently Jackson and Lu (1994) identified two distinct zones in the statolith of the demersal Antarctic squid *Psychroteuthis glacialis*. In this species, the inner zone consisted of less well defined increments that changed abruptly into an outer zone with very distinct increments. These differences were suggested as also possibly representing two phases of growth (pelagic and demersal). For such species, it might thus be possible to determine the period of time that an individual spends in the open water before "settling." Such information has been successfully utilised in fish otolith studies (Victor 1986; Cowen 1991; Victor 1991; Wellington and Victor 1992) and has proved to be an extremely important and useful environmental tool.

Much of what has been obtained from statolith increment analysis could be considered preliminary in nature. The research is now at a stage where more powerful applications can be made with incremental techniques. With the development of new computer-based image-analysis systems (e.g., Macy 1992; Campana 1992), it is now possible to carry out more detailed increment width analysis. This could provide a means to detect daily variation in growth rates. Image-analysis systems should also be useful for facilitating increment counts. By using enhanced video images, it may be possible to consider alternative validation techniques (e.g., marginal increment width analysis). This has been used successfully to validate the timing of otolith increment formation in some fish species from samples which have been collected over a 24-h period (e.g., Jenkins 1987; Jenkins and Davis 1990; Gartner 1991). Because of the general small size and narrow increments in most statoliths compared with fish otoliths, this technique may not have been a viable approach to validation. However, new image-analysis systems may now make this a viable option especially for fast-growing tropical species (which have wider increments).

As mentioned earlier, there is a need for continued validation studies. Obtaining information on increment periodicity for a species near to its maximum size would be particularly useful. The studies to date provide encouraging results that increments are produced daily in many species. However, the body of evidence is still relatively small and there is a great need to continue validation experiments on more species and covering a larger size range. For age studies being carried out on species for which there is no validation evidence, researchers should clearly understand the constraints and limitations of their data sets. However, this should not restrict researchers from exploring what information is available within the statolith microstructure.

Currently, there has been little emphasis on growth during the early paralarval phase of growth in many squid species (see Balch et al. 1988; Laptikohovsky et al. 1993; Bigelow 1992; Bigelow and Landgraf 1993). Research on this portion of the life cycle is particularly needed as statolith increment analysis has contradicted early theories that suggested that young squid were thought to grow rapidly to "speed them through" a vulnerable juvenile period (Calow 1987). In contrast, squid appear to spend a larger proportion of their life cycle as small individuals (e.g., Fig. 3D; see also Jackson 1991a; Jackson and Choat 1992). Age information during the young stages would provide a greater body of evidence on growth during this interesting period of squid growth.

There is a need for researchers to use statistical stringency for both validation and increment counting techniques (see Natsukari et al. 1991). Any studies employing ageing techniques should provide information on the precision of their age estimates. This should take the form of replicate counts per statolith or the calculation of an error estimate for counts carried out that are not replicated.

Statolith size or weight may also reveal information about a squid's past history, especially when combined with ageing studies. Jackson (1991a) found that there was an uncoupling between mantle length and statolith length in *Loligo chinensis*, in that slower growing, winter individuals had larger statoliths than their faster growing summer counterparts. The results of this analysis paralleled results of fish otolith studies that also documented that faster growing fish have smaller otoliths than similar-sized slow growing fish (e.g., Secor and Dean 1989; Reznick et al. 1989; Wright et al. 1990). Analysis of length or weight of statoliths may, therefore, reveal past growth histories without even obtaining age information. Further studies should consider the significance of statolith size or weight measurements in revealing past growth histories. Moreover, combining statolith length–weight measurements with increment width analysis could provide a wealth of (as yet untapped) information.

Because the oceanic and deepwater squids compose an enormously huge biomass (see Clarke 1983) of many species, they must play an important role in the world's oceanic ecosystem. However, currently very little is known of the biology of many of these species, and indeed the biology of many shelf species is only now becoming better known. There is thus the need to obtain biological information of this important (but often ignored) component of the world's marine ecosystem.

In summary, studies to date show that statolith ageing studies should continue to provide useful and important information on age, growth, maturity, and life-history parameters of squids and some sepioids. Because much of the work dealing with statolith age analysis has been preliminary in scope, there is need for continued work in a number of areas. These include: (i) undertaking more comprehensive statolith ageing studies on a larger number of species including oceanic squids to obtain life-history information for poorly known species; (ii) investigating further the presence of statolith increments in other cephalopods (e.g., other sepioids); (iii) studying more comprehensively the validation of increment periodicity, including longer term culture experiments covering all phases of the life cycle, (iv) emphasising growth modelling to develop more accurate and robust models of squid growth; (v) looking into more powerful ecological uses of statolith increments, such as temporal or geographical variations in growth responses to ambient biological or physical features, and how increment width patterns within the statolith microstructure may reflect ambient changes in food availability, temperature, etc.; (vi) obtaining age-specific information on the timing of maturation and the duration of spawning; (vii) considering the significance of other features within the statolith microstructure such as obvious zones or prominent checks that might provide information on past habitats or perturbations; and (viii) considering

how other parameters such as statolith length or weight might vary as a result of different past growth histories.

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Restricted Movement in Resident Stream Salmonids: A Paradigm Lost?

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Gerking (1959. Biol. Rev. 34: 221–242) proposed a theory about the restricted movement of stream fishes that may be considered a paradigm in salmonid biology. The restricted movement paradigm (our term) hold that resident stream salmonids are sedentary. Numerous studies have supported the restricted movement paradigm, but nearly all have relied on the recapture of marked fish from the same areas in which they were released, an approach we believe is biased against detecting movement. We found substantial movement of trout in streams in Colorado and Wyoming using two-way weirs and radio telemetry. A review of the research on Lawrence Creek, Wisconsin, also showed that movement was important in the response of the trout population to habitat enhancement. Movement of resident stream fish has profound implications for research (e.g., measuring production and habitat models) and management (e.g., habitat enhancement, special regulations, and stocking hatchery fish). Methods capable of detecting fish movement could be incorporated into many studies to assess its importance in systems of interest. New theories and experiments are needed to understand the mechanisms that cause stream salmonids to move.

Gerking (1959. Biol. Rev. 34: 221–242) a proposé une théorie sur la limitation du déplacement des poissons dans les cours d'eau que nous croyons être un paradigme en biologie des salmonidés. Selon cette théorie, nommée par nous paradigme de la limitation du déplacement, les salmonidés résidents des cours d'eau seraient sédentaires. De nombreuses études ont appuyé ce paradigme, mais presque toutes étaient fondées sur la recapture de poissons marqués dans les zones mêmes où ils avaient été libérés, une approche que nous croyons biaisée en ce qui concerne la détection du déplacement. Nous avons constaté un déplacement substantiel de truites dans des cours d'eau du Colorado et du Wyoming à l'aide de bordiques à deux voies et de la radiotélémesure. Une revue de la recherche effectuée dans le Lawrence Creek au Wisconsin a également montré que le déplacement était important dans la réponse de la population de truites à l'enrichissement de l'habitat. Le déplacement des poissons résidents des cours d'eau comporte d'importantes implications en recherche (p. ex., mesure de la production et modèles d'habitats) et en gestion (p. ex., enrichissement de l'habitat, réglementation particulière et stockage des écloseries). Des méthodes permettant de déceler le déplacement du poisson pourraient être intégrées à de nombreuses études afin d'évaluer son importance dans les systèmes en cause. De nouvelles théories et de nouvelles expériences sont nécessaires à la compréhension des mécanismes à l'origine du déplacement des salmonidés dans les cours d'eau.

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In a paper titled, *The restricted movement of fish populations*, Gerking (1959) proposed a theory that guided much of the research into the dynamics of stream fish populations for the next 30 years. Many studies published since Gerking (1959) claim to support the theory, which in our view could be considered a paradigm (sensu Kuhn 1970). The main tenet of this restricted movement paradigm (RMP, our term) is that adult stream fish are sedentary, often spending their entire lives within a single pool (e.g., Bachman 1984) or within a stream reach no longer than 20 m (e.g., Miller 1957).

In contrast to the RMP, there is increasing evidence that movement is relatively common in populations of stream-resident salmonids. Research we are conducting in high-elevation streams in the Rocky Mountains of Colorado and

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TABLE 1. Some widely recognized movements of resident stream salmonids.

Behavior and observed characteristics	Sources
1. Passive fry dispersal with flow	Elliott 1966; Ottawa and Clarke 1981; Crisp and Carling 1982; Ottaway and Forrest 1983; Irving 1986; Elliott 1987; Heggenes and Traaen 1988
2. Active fry dispersal, possibly mediated by social dominance effects	Kalleberg 1958; Chapman 1962; Solomon and Templeton 1976; Heland 1980a, 1980b; Elliott 1987; Heggenes 1988a; Elliott 1990; Crisp and Hurley 1991
3. Limited fry dispersal in closely juxtaposed habitats	June 1981; Moore and Gregory 1988a, 1988b; Trotter 1989; Beard and Carline 1991
4. Specialized patterns of fry and juvenile dispersal in unique habitats	Northcote 1962, 1969, 1981; Northcote and Kelso 1981; Northcote and Hartman 1988
5. Movements related to ontogenetic shifts in microhabitat use, possibly to increase rate of food intake or avoid competition by habitat segregation	Newman 1956; Saunders and Smith 1962a; Hartman 1965; Egglishaw 1967; Shetter 1968; Chapman and Bjornn 1969; Solomon and Templeton 1976; Alexander 1977; Stauffer 1980; Fausch and White 1981; Bachman 1982; Moore and Gregory 1988a, 1988b; Clapp et al. 1990
6. Diel movements from feeding to resting positions	Elson 1942; Hoar 1953; Lindroth 1955; Newman 1956; Kalleberg 1958; Chapman 1962; Northcote 1962; Swift 1962, 1964; Mason 1966; Edmundson et al. 1968; Chapman and Bjornn 1969; Campbell and Neuner 1985; Clapp et al. 1990
7. Movements related to fish having different microhabitats preferences at different water temperatures	Chapman and Bjornn 1969; Bjornn et al. 1977; Smith and Li 1983; Campbell and Neuner 1985; Moyle and Vondracek 1985; Sheppard and Johnson 1985; Baltz et al. 1987
8. Seasonal movements between summer and winter habitat locations (distances moved may be short if summer and winter habitats are closely juxtaposed, or extensive (>100 km) if required habitats are widely dispersed)	Cooper 1953; Smith and Saunders 1958, 1967; Hartman 1963, 1965; Chapman and Bjornn 1969; Hunt 1969b; Bustard and Narver 1975; Craig and Poulin 1975; Solomon and Templeton 1976; Gibson 1978; Leclerc and Power 1980; Montgomery et al. 1983; Rimmer et al. 1983; Campbell and Neuner 1985; Sheppard and Johnson 1985; Chisholm et al. 1987; Hartman and Brown 1987; Hillman et al. 1987; Cunjak 1988; Cunjak et al. 1989; Craig 1989; Trotter 1989; Clapp et al. 1990; Nakano et al. 1990; Näslund 1990; Baltz et al. 1991; Meyers et al. 1992; West et al. 1992
9. Potadromous spawning movements predominantly upstream over relatively long distances	McFadden 1961; Harden-Jones 1968; Solomon and Templeton 1976; Craig 1978; Leclerc and Power 1980; Meyers et al. 1992
10. Potadromous spawning movements in all directions over relatively short distances (when spawning and rearing habitats are interspersed)	Northcote and Hartman 1988; Moore and Gregory 1988a; Trotter 1989; Nakano et al. 1990; Beard and Carline 1991
11. Homing movements following displacement	Miller 1954; Saunders and Smith 1962b; Harcup et al. 1984; Halvorsen and Stabell 1990

Wyoming supports this view (Riley et al. 1992; Young 1994) and calls the RMP into question for these systems. Furthermore, in previous studies supporting the RMP, we find that one experimental approach was used almost exclusively, an approach that we believe has led to erroneous conclusions supporting restricted movement. In this paper we review the literature related to restricted movement, summarize the methodological problems we perceive, and provide new information to suggest that the paradigm is not as robust as currently believed. Our review focuses primarily on wild salmonids (see Cresswell 1981 for a review of hatchery salmonid movements), but includes examples from other taxa where appropriate.

Restricted Movement Paradigm

The literature on resident stream salmonids, considered as a whole, indicates that adult fish establish restricted territories for feeding and remain there. Although some types of movement are acknowledged (Table 1), they are often characterized as specialized behaviors which interrupt the "normal" sedentary behavior of the fish. These behaviors include the passive and active dispersal of trout fry, various movements related to ontogenetic shifts in habitat use or diet, diel movements between feeding and resting areas, and seasonal and spawning movements. Certainly, other important movement behaviors could be added to this list (see Northcote 1992 for a detailed review). Overall, movement behavior appears to be extremely plastic and presumably adaptive in a wide variety of environmental situations.

Although the tenets of the RMP can be stated succinctly, it is clear that there can be no universal definition of restricted movement. If fish are "restricted" in their movements, how far would they have to move to show "unrestricted" movement, and what percentage would have to move for the population to be considered mobile? These

TABLE 2. Reach length, time between contacts, conclusions drawn from recaptured fish, and percentage of marked fish that were not recaptured in studies of salmonid movement. Reach length indicates the length of the "home reach" (HR) from which fish were captured, batchmarked, and released. Alternatively, IND(X) indicates that individually marked fish could be tracked to within X m. Time between contacts refers to the minimum time between any two samples. If multiple samples were taken, the value in parentheses is the total study duration. Conclusions from recaptures were based strictly on those fish that were initially marked and subsequently recaptured, and were usually reported by the authors as the main results from their study. Data that were not reported and could not be calculated from information in the original text or tables are designated NR. Ranges indicate that data were from multiple years, multiple locations, or both. Commas separate results from distinct portions of the same study. Entries are grouped by species and run most to least commonly studied.

Species	Reach length (m)	Time between contacts (d)	Conclusions from recaptures	Percentage not recaptured	Source
S. trutta	65	365	91% in HR	85	Schuck 1945
S. trutta	274	90	95% in HR	94	Allen 1951
S. trutta	46	90	70–84% in HR	53	Stefanich 1952
S. trutta	IND (150)	1 (1825)	56–90% within 1600 m	91	Shetter 1968
S. trutta	100–183	61 (2190)	64% in HR	74	Burnet 1969
S. trutta	4345	1 (1095)	50% in HR	90	Klein 1974
S. trutta	61	80, 365	67, 46% in HR	NR, 62	Mense 1975
S. trutta	100	90, 450	71, 65% within 100 m	NR	Solomon and Templeton 1976
S. trutta	20	29 (739)	86% within 60 m	65	Jackson 1980
S. trutta	10–28.6	7 (42)	68–93% within 15 m	25–55	Harcup et al. 1984
S. trutta	IND (3)	14 (575)	61% within 50 m	74	Heggenes 1988b
S. trutta	12.5–25	20 (80)	85–89% within 50 m	NR	Hesthagen 1988
S. trutta	305	240	71% in HR	73	Larson 1988
S. trutta	IND (2)	2 (346)	mean movement = 386 m	77[a]	Clapp et al. 1990
S. trutta	IND (161)	14 (165)	78% within 800 m	44[a]	Meyers et al. 1992
S. fontinalis	46	90	100% in HR	80	Stefanich 1952
S. fontinalis	27	28, 35	13, 14% in HR	86, 87	Smith and Saunders 1958
S. fontinalis	IND (150)	1 (365)	88% within 1600 m	90	Shetter 1968
S. fontinalis	300–1500	1 (425)	"limited movement"	NR	Leclerc and Power 1980
S. fontinalis	300	365 (730)	56% in HR	75	Moore et al. 1985
S. fontinalis	IND (1.2)	4 (152)	mean movement = 86 m	13[a]	Chisholm et al. 1987
S. fontinalis	250	365 (1095)	83% in HR	58–78	Riley et al. 1992
O. mykiss	46	90	62–75% in HR	54	Stefanich 1952
O. mykiss	4345	1 (1095)	30% in HR	88	Klein 1974
O. mykiss[b]	IND (<1 m)	1 (14)	63–68% within 6 m	29–80	Edmundson et al. 1968
O. mykiss	165–425	120 (956)	97% in HR	33	Cargill 1980
Three species[c]	30–32	30 (90)	3–53% in HR	44–94	Shetter and Hazzard 1938
Three species[c]	91	36 (375)	90% within 150 m	75–97	Holton 1953
O. clarki	161	1 (260)	100% in HR	89	Fleener 1951
O. clarki	9–18	30 (850)	67% in HR after 2 yr	41	Miller 1957
O. clarki	IND (1600)	1 (1245)	25% within 1600 m	89	Bjornn and Mallet 1964
O. clarki	IND (3)	14(240)	88% within 3 m	40	Heggenes et al. 1991
S. salar[b]	5–100	14 (123)	94% "near home"	24	Saunders and Gee 1964
S. salar[b]	300–1500	1 (425)	"limited movement"	NR	Leclerc and Power 1980
S. salar[b]	12.5–25	20 (55)	93–96% within 50 m	NR	Hesthagen 1988
O. gilae	IND (10)	90 (240)	75% within 100 m	70	Rinne 1982
O. masou	1–30	2 (605)	33–90% within HR in 30 d	56	Nakano et al. 1990

[a]Percentage of all radio tags implanted that were never relocated in a live fish.
[b]Juveniles of anadromous stocks.
[c]*S. trutta*, *S. fontinalis*, and *O. mykiss*.

questions have no objective answers because all the terms are relative. Therefore, the focus of our paper is not so much to define criteria for fish movement, but to explore how we as scientists and managers think about it. We believe the predominant view is that stream fish are "sedentary."

To justify this assertion, we point to the most common way resident stream fish are studied and managed. In both research and management, the "target" population is almost always defined as those individuals inhabiting a designated stream reach. Such a definition implicitly assumes only limited movement of fish in and out of the reach. Would a researcher studying a pelagic species in a large lake define the study population as all the fish in a relatively small volume of water in the center of the lake? Our point is not that

studying stream fish populations in specific reaches is incorrect, but that fish movement is rarely explicitly considered when study reaches are defined. To us, this implies that the RMP is widely accepted by scientists.

By saying that the RMP is widely accepted, we do not mean that the view is universal, nor that scientists strongly resist the idea of fish movement. More accurately, restricted movement is a de facto null hypothesis, one that scientists are willing to reject when presented with specific evidence to the contrary from their streams of interest. However, because fish movement is not routinely studied as part of research and management activities, the RMP often may be accepted simply because there was no attempt to refute it. Furthermore, we believe that information indicating that resident fish do move often goes unrecognized because biologists are predisposed to accept the RMP.

In contrast to the RMP, we believe that movement in resident stream salmonids, even during nonbreeding, summer feeding periods, is a potentially common and important phenomenon. This is not to suggest that all, or even most, fish are mobile, but simply that it is inappropriate to proceed with management and research without explicitly considering the potential for fish movement. In addition, because movement is acknowledged to occur for a wide variety of reasons (Table 1), we believe the RMP provides too narrow a focus to one's thinking. Many studies can be cited in support of the RMP, but we find that the methods used produce an unintentional bias against the detection of movement. Below, we summarize some of these studies and explain why we think it is incorrect to conclude from them that resident salmonids are sedentary.

Data and a Problem

Studies related to movement of resident stream fish have been conducted many times over the past 55 years. Although the method of capture varied, the basic study design did not. Fish were collected within various study sections, marked to indicated the section of capture (or were individually marked and the exact capture location recorded), released, and recaptured during subsequent sampling periods. Conclusions regarding movement were based on the percentage of recaptures made within the "home" section, or on the distances moved by individual fish. Many influential studies using these general methods have been used to support the RMP, but relatively few reported that fish movement was common (Table 2; the column labeled "Conclusions from recaptures" most accurately reflects the conclusions the authors made about fish movement).

Part of the reason different studies yielded different conclusions regarding the frequency and magnitude of movement is due to variations in study design. For example, most research supporting the RMP involved repeated sampling of the same stream reaches to recapture marked fish. Alternatively, studies documenting long-range fish movements generally used radio telemetry or other methods that permit recapturing individuals over long distances. That methods can influence results was not missed by Gerking (1959, p. 225), who wrote, "The design of the experiment which is intended to yield information about movements of fish may introduce a bias in favour or against the home range. This results from the fact that the size of the home range is not known before the experiment begins. If a large area is chosen when the size of the home range is small, a high proportion of the fish will be found in the sampling area. If the study area is small in relation to the home range, very few will be found in successive samples....any quantitative expression about the size of the home range and the degree of straying describes the techniques of the investigator as much as the behaviour of the fish."

In an excellent paper reviewing the available ecological models for describing animal movements (most of which show restricted movement to be the norm), Porter and Dooley (1993) found that most study designs were biased against the detection of movement. In their conclusions they reiterated Gerking's (1959) warning, "Unfortunately, our own results suggest that the models may be much more successful at describing the way ecologists measure movements than the way animals move."

Although Gerking (1959) and Porter and Dooley (1993) correctly emphasized problems in choosing the size of the study area, our main concern about studies supporting the RMP is that conclusions were based only on the recapture of marked individuals from the areas where they were originally released. A consequence is that, compared with the number of fish originally marked, the number recaptured was usually low (Table 2). Although it is true that a high percentage of recaptures was made near the location of original capture, it is equally important that in 26 of 33 studies (78%) for which data were available, more than half of the fish originally marked were never recaptured, and in 14 (42%), 75% or more were not recaptured.

Most authors do not comment on the fraction of the population not recaptured, and it sometimes went unreported altogether. Low recapture rates are to be expected given the inherent difficulty in collecting fish, and the high mortality stream salmonids generally experience (e.g., McFadden 1961; Alexander 1979). If the authors do discuss these missing individuals, it is usually assumed that they died (e.g., Stefanich 1952; Mense 1975) or moved due to handling and marking stress (Gerking 1959). However, the short periods between samples in many of the studies (i.e., 24 of 37 were less than 60 d; Table 2) make it unlikely that mortality could account for all the missing individuals. Similarly, efficient collection and handling methods have been employed in more recent studies, but the percentage recaptured remains low (e.g., Riley et al. 1992). While the inability to recapture a high proportion (say, >85%) of marked fish does not prove that movement is occurring, we believe that it is important to recognize the inherent circularity in concluding that fish do not move based on studies that concentrated recapture efforts almost exclusively in the same areas in which fish were released. The large number of fish never recaptured certainly leaves open the possibility that many fish moved beyond the study boundaries.

Some indication that the results were artifacts of the methods comes from studies where the turnover of individuals in a limited stream reach has been measured. This approach involves marking a high proportion of the fish in a reach during initial sampling, and making inferences about the frequency of movement based on the relative proportion of marked and unmarked fish found during resampling. In these studies, it is common for marked fish to be rapidly replaced by unmarked ones (Shetter and Hazzard 1938; Smith and Saunders 1958; Decker and Erman 1992; Cunjak and Randall 1993). These examples demonstrate that reliable information about movement can be gotten from a "stream reach" approach, so long as

inferences are not based exclusively on marked fish. Alternative methods which allow fish to be recaptured over large spatial scales (i.e., radio telemetry) are also important and show almost universally that some individuals move long distances (e.g., Shetter 1968; Clapp et al. 1990; Meyers et al. 1992). Clearly, conclusions drawn about fish movement depend on the spatial and temporal scale studied.

Static versus Mobile Dichotomy

The evidence that some fish move very little and others move a great deal led Funk (1955) to propose the concept of "sedentary" (static) and "mobile" fractions of fish populations. Stott (1967) developed a graphical method to identify and quantify these subpopulations. Solomon and Templeton (1976), the first authors to apply the technique to salmonids, found mobile and static subpopulations of brown trout (*Salmo trutta*) in an English chalk stream. They did not estimate the size of the mobile fraction, but described it as "small." Harcup et al. (1984) calculated that the mobile fraction in another English brown trout population ranged between 17 and 71% (from their Fig. 4), depending on the time interval between observations (range 7–14 d). Hesthagen (1988) estimated that 15–20% of individuals in a brown trout population in Norway were mobile. Heggenes et al. (1991) reported a "small" mobile fraction in a coastal cutthroat trout (*Oncorhynchus clarki clarki*) population in British Columbia, but did not quantify its size.

Other authors have concluded that two subpopulations were present by using techniques other than those proposed by Stott (1967). Flick and Webster (1975) found that brook trout (*Salvelinus fontinalis*) captured moving upstream through two-way weirs in a New York stream were only rarely recaptured moving downstream during the same season. By contrast, 79% of fish moving downstream were soon recaptured moving upstream. To Flick and Webster (1975), this was "indicative of a resident as well as migratory segment of the population." Jackson (1980) concluded that the spatial distribution of brown trout recaptures in an Australian stream suggested a "mobile group moving beyond the restricted home range of brown trout". Using similar reasoning Cargill (1980) drew the same conclusion for rainbow trout (*O. mykiss*) in Minnesota, as did Halvorsen and Stabell (1990) for brown trout in Norway.

Although the static versus mobile concept includes fish movement, it also implies that individual fish fit into one category or the other (Funk 1955; Gerking 1959; Jenkins 1969; Bachman 1984). Harcup et al. (1984) provide data to suggest that this is not necessarily true. When tracking individually tagged fish in each of 2 yr, they found frequent switching behavior in which formerly sedentary fish moved, and formerly mobile fish became sedentary. In fact, a median of 33% (range 17–66%, $n = 8$ experiments; from fig. 4 of Harcup et al. 1984) of recaptured fish had switched behaviors between surveys spaced 7–21 d apart. This implies that movement behavior may be plastic, allowing individual fish to adapt to variable environmental conditions. For this reason, we believe that attention should be focused on the mechanisms determining the frequency and extent of fish movement, rather than on the RMP or the static versus mobile dichotomy.

A Matter of Emphasis

Although biologists acknowledge that some fish move, greater emphasis is almost invariably placed on those that do not. This is natural in that repeated observations of the same fish seem inherently more informative, and lend themselves to more detailed analyses, than single observations of many different fish. This is reflected in the terminology applied to the mobile fish. Gerking (1959) labeled them as "strays." Jenkins (1969) used the term "transients" and believed them to be subdominants which could not successfully defend a territory.

It may be difficult to measure the mobile population, but that does not mean that it is biologically unimportant. For example, Näslund (1990; Näslund et al. 1993) demonstrated that mobile Arctic char (*Salvelinus alpinus*) were able to find and exploit new feeding opportunities in two recently eutrophied lakes 5 km upstream from the oligotrophic "home" lake. As a result, mobile fish grew faster and matured 2 yr sooner than the sedentary fish. Burgess and Bider (1980) demonstrated that movement played an important role in population responses of brook trout to habitat enhancement in a Quebec stream, a topic we discuss in more detail below.

Paradigm Lost

Data from Rocky Mountain Streams

Careful analysis of our data collected in the Rocky Mountains of Colorado and Wyoming, and that of other investigators in other regions, revealed patterns inconsistent with restricted movement and forced us to question the paradigm. Three of the authors (K.D. Fausch, C. Gowan, and C. Riley) have been conducting a long-term study of trout population response to habitat enhancement using low log weirs (log drop structures) in six Colorado mountain streams (see Riley and Fausch 1995 for details). In 1987, 500 m of relatively homogeneous riffle and glide habitat were selected for study for each of five of the six streams. Separate three-pass removal population estimates were made annually during late summer low flows in each 250-m half after blocking the ends with seines (see Riley and Fausch 1992). During summer 1988, 10 log drop structures were installed in a randomly-chosen 250-m half designated as the treatment section, and the other half served as the unmanipulated control section. In the sixth stream, all methods were the same except 250-m control sections were selected both upstream and downstream of a 375-m treatment reach with 15 logs.

During the annual surveys, all trout larger than 69 mm total length (TL; approximately age 1 and older) were given fin clips (adipose or left pelvic) unique to either the treatment or control section of each stream. Handling mortality was extremely low for fish held in baskets overnight following electrofishing and marking (0.5% for 10 experiments, $n =$ 2122 fish; Riley et al. 1992). Direct monitoring of fish movements before and after electrofishing using weirs on two streams showed no increased movement out of the study reaches (C. Gowan and K.D. Fausch, unpublished data). Because our capture efficiency was high (a median of 93% of age-1 fish and 98% of age-2 and older fish after three electrofishing passes; Riley and Fausch 1992; Riley et al. 1992), and because undetected fin regeneration almost never occurred (judging from recaptured fish with both tags and finclips, K.D. Fausch and S.C. Riley, unpublished data), most fish older than age 1 that are captured each year should have borne marks. However, for 22 annual surveys between 1988 and 1990, a median of 52% (range 17.4–84.3%) of

adult trout were unmarked, indicating a high rate of movement into the study reaches (Riley et al. 1992). In fact, it appears that fish movement into the treatment sections was primarily responsible for the rapid population increase after habitat enhancement (Riley and Fausch 1995). However, the treatment response did not result from trout moving from control to treatment sections, but primarily from unmarked fish apparently moving from longer distances. For this reason, we believe it is incorrect to say that the treatment section is attracting fish (in the sense that the fish "detect" it at a distance and respond by moving), although it is clearly attractive to fish once they encounter it (Riley et al. 1992). Our continuing research is focusing on why fish are moving and the distances they travel when they do.

The data reported by Riley et al. (1992) also can be used to demonstrate the problems inherent in drawing conclusions about fish movement solely from recaptured fish. In our studies, it was possible to detect fish movement between the treatment and control sections owing to the unique marks each group received. Of the fish bearing marks from a previous capture, an average of 83% (range 64–100%, $n = 22$ samples) remained in their home 250-m sections between years (calculated from table 2 in Riley et al. 1992), which could be interpreted as evidence for restricted movement. However, the large influx of unmarked fish into the study reaches between years demonstrates that this conclusion is in error. We have also operated two-way weirs between mid-July and late-September at the three section boundaries on two of the six streams since 1991 and usually captured more fish moving during the 7–15 wk trapping periods than were present in the study reach during the annual population estimates (Riley et al. 1992; Gowan and Fausch, unpublished data). In short, fish movement in our streams is not evident based on the percentage of recaptures that "stayed home," but it is very apparent when inferences are based on turnover of individuals within the populations, or when fish movements are measured directly. For this reason, it is important that future studies employ collection methods with a high probability of capturing fish. If most of the fish are captured and marked during the initial sampling, then large numbers of unmarked fish captured during resampling clearly suggest that immigration is occurring. In this way, the typical stream-reach study design can still be used to detect fish movement, even if only a small percentage of marked fish are ever recaptured.

Independent of the studies just described, Young (1994) investigated the movements of brown trout in two Wyoming streams. Fish of 250–530 mm TL were implanted with transmitters and monitored twice weekly throughout 1991. Thirty-seven of the 54 monitored fish had home ranges (the distance between the upstream- and downstream-most detections) greater than 50 m, and 16 had home ranges greater than 300 m. Median weekly movements of brown trout ranged from 12 to 51 m, with the greatest mobility in autumn. Brown trout <340 mm tended to move less than 20 m per week, whereas larger fish often moved over 50 m per week. In hourly monitoring over the 24-h cycle, some individual brown trout moved more than 1000 m (M.K. Young, unpublished data).

Three of the larger fish had home ranges from 23 to 96 km, which included downstream movements into a large river. To study this movement in more detail, a two-way fish trap was installed in one of the two study tributaries and monitored daily in summer 1992. An upstream movement of large brown trout (mean length = 376 mm) reached its maximum in late July. Similar-sized fish were captured near the fish trap in late September 1992 and implanted with radio transmitters. There fish remained in the stream throughout winter, and moved downstream over 400 m to a large beaver pond by early May. Most then moved farther downstream to the river during high spring flows. These patterns imply the existence of a fluvial population of large brown trout that moves from the river to the stream in summer, spends up to 9 mo in the stream, then returns to the river during the snowmelt runoff.

Similar studies of smaller (170–237 mm TL) Colorado River cutthroat trout (*O. c. pleuriticus*) in a Wyoming drainage revealed home ranges in June through early August that often exceeded 500 m (M.K. Young, unpublished data). Furthermore, the direction of movement was unpredictable; fish moved both upstream and downstream in a third-order stream after descending from tributaries where they had originally been captured. In 24-h monitoring, some individuals moved more than 100 m (M.K. Young, unpublished data).

Data from Other Regions

Careful inspection of research publications by other investigators also indicates that movement is important in stream-resident salmonid populations in other regions. For example, Burgess (1985) and Burgess and Bider (1980) reported that net upstream immigration into paired 100-m sections of a divided Quebec stream was high, but that net upstream emigration was much lower from the one where habitat was enhanced by adding pools and overhead cover.

One of the most intensive research projects was conducted on Lawrence Creek, Wisconsin, where the brook trout population was studied for 18 yr (1953–70). During this time different fishing regulations were tested (McFadden 1961; Hunt et al. 1962; Hunt 1970), habitat enhancement was evaluated (Hunt 1969a, 1971, 1976), and production and other trout population processes measured (Hunt 1965, 1966, 1969b, 1974; Hunt and Brynildson 1964). The entire reach of stream suitable for trout, starting at the confluence of two small tributaries upstream and discharging into a small warmwater reservoir 5.4 km downstream, was divided in four contiguous sections (A–D, starting upstream) each 1.1–1.7 km long. The trout population in each section was estimated by two-pass (Petersen) mark–recapture electrofishing each April, June, and September (spring and fall only before 1959). At least 75% of the age-0 trout were captured during June and September each year, and marked by fin clips to denote their section of origin and year-class (Hunt 1974).

Most spawning occurred in upstream sections A and B, which contained about 80% of redds during 1958–62 (Hunt 1965). Age-0 trout dispersed primarily downstream, but also upstream, so that by September each section contained some fish from all other sections. For example, 35% of age-0 trout marked marked in June 1959 were recaptured in a different section in September. Immigrants accounted for 25% of age-0 trout in sections A and B and 55% in sections C and D in September 1959.

Adult trout also moved. Hunt (1974) reported that trout moved to upstream sections to spawn in the fall and to larger pools downstream to overwinter. Section A (farthest upstream) was designated as a trout refuge and closed

to angling during 1956–60 (Hunt and Brynildson 1964), during which the population increased markedly from 868 to 2157 age-1 and older trout and then declined to 356 trout by 1960 (Hunt 1971). Although only 5–11% of the total population in section A were immigrants in any given sample, a total of 2789 adult trout marked in downstream sections was recaptured there over the 5-yr period, which was more than the highest population recorded during the period.

Movement also apparently played a strong role in the brook trout population response to habitat enhancement in Lawrence Creek. After a 3-yr pre-treatment measurement period (1961–63), habitat in section A was enhanced in 1964 using structures that combined current deflectors and overhanging bank cover (Hunt 1971). Trout abundance, biomass, and production increased dramatically in section A in the subsequent 6 yr (1965–70; Hunt 1971, 1976), and abundance of age-2 and older trout increased much more than juveniles. Annual fall recruitment of age-0 trout fluctuated widely but, on average, was similar during the 3 yr before and after enhancement in section A and declined after enhancement in the three downstream sections. Based on these data, Hunt (1971) concluded that the habitat enhancement caused the trout population to increase primarily by increased overwinter survival, rather than increased recruitment, with the benefits accruing primarily to older trout.

Despite the emphasis on increased "apparent" overwinter survival, several lines of evidence suggest that movement was also an important mechanism causing increased trout abundance. Hunt (1969a) reported that overwinter emigration from section A was 64% less after enhancement than before, and oversummer emigration was 11% less, despite higher trout density after enhancement. Similarly, Chapman and Bjornn (1969, Table 2) presented data supplied by Hunt showing that 29–30% of age-1 and older trout in section A in April were immigrants both before and after enhancement, despite the 65% increase in abundance of these age-classes of trout after habitat development (Hunt 1971).

An interesting phenomenon that Hunt (1971) did not discuss was the increase in trout abundance in sections adjacent to the one where habitat was enhanced, and the progressive decline in these increases with distance. After habitat enhancement, abundance of age-1 and older trout in April in section A–C increased 65, 38, and 19%, respectively, but declined 28% in section D, the farthest downstream. This trend held for all age classes, and for most measures of biomass and production as well. Moreover, the increases could not be explained by strong year-classes that affected post-treatment abundance more than pre-treatment. When combined with the results discussed above, there data lead us to suspect that trout readily moved among sections in Lawrence Creek, so that trout from downstream sections rapidly encountered the better habitat and the overwinter survival benefits produced by the habitat enhancement were readily transferred to adjacent sections. Riley and Fausch (1995) reported similar increases in trout populations in control sections adjacent to those where the log drop structures were installed, in all six Colorado mountain streams they studied.

Hunt (1974) presented a final line of evidence indicating that brook trout movement was important. He found that trout production (i.e., elaboration of new tissue, calculated as the product of mean monthly biomass and growth rate) varied widely across years for each of the four sections, especially in section A after habitat enhancement. However, production was remarkably consistent over an 11-yr period for the reach as a whole because increased production in section A was counterbalanced by decreased production downstream. Although Hunt discussed upstream movement of trout, and stated that downstream emigration from section A decreased after habitat enhancement, he did not emphasize movement as a likely mechanism stabilizing streamwide production. In Hunt's (1974, p. 12) words, "... it is particularly striking that the trout population in Lawrence Creek appeared to function as a homeostatic unit on a streamwide basis. Somehow the level of production in any one section or age group was related to production that year in other sections and other age groups."

Moreover, despite the evidence supporting the importance of increased overwinter survival *and* movement in the response of the Lawrence Creek brook trout population to habitat enhancement (see Hunt 1976), we believe that most biologists and managers have focused on increased overwinter survival as the principle finding of Hunt's work. In accordance with the RMP, in situ survival and production of resident trout is the assumed mechanism by which trout populations increase after habitat enhancement.

Implications for Resfearch and Management

As previously discussed, research and management typically involves defining the "target" population of interest as those individuals inhabiting a designated stream reach. Our concern over uncritical acceptance of the RMP lead us to consider the implications of mistakenly operating under this theory as a researcher or manager.

The most serious consequences of the RMP for research on resident stream salmonids stem from the assumption that different stream reaches can be considered as independent units (e.g., Bohlin 1978). For example, Hunt (1974) emphasized the potential bias of extrapolating annual production estimated from any one of the four study reaches in Lawrence Creek to the entire stream. The point is that the definition of fish production becomes ambiguous if immigration and emigration rates are high. How should fish tissue "elaborated" via immigration be treated in the analysis? Hunt (1974) was largely able to solve this problem by estimating production for an entire stream, but this is not a viable option for most managers. Addicott et al. (1987) detail methods for defining the "ecological neighborhood" within which an organism completes certain life-history processes such as foraging or reproduction, an approach which may be useful in defining an appropriate reach for fish production analyses.

Significant effort has been devoted to developing models that predict standing crops of stream fish from habitat variables (Fausch et al. 1988). These models have the implicit assumption that fish abundance in a given reach is directly related to the habitat there, and often also assume that fish populations respond instantaneously to habitat changes. If fish move, the time lag between changes in habitat and response by the population is likely to be relatively short, compared with time lags due to changes in survival or fecundity, thereby supporting the basic model assumptions. However, if, as a result of movement, the fish population being modeled is governed by unmeasured habitat conditions in other stream reaches, then the habitat models developed from a single

reach becomes less useful and attempts to validate them may be futile (Decker and Erman 1992). Sale (1991, p. 566) describes similar consequences for management of coral reef fish communities, which are thought to be open, non-equilibrial systems driven by chance recruitment of juveniles from the ocean ichthyoplankton (i.e., the lottery hypothesis): "Under these circumstances, local densities are not necessarily set by the limits of locally available resources, and local harvest may have little effect on future local recruitment. At the same time, overexploitation in one location may have severe effects on future recruitment to other, possibly quite distant sites. At present it is simply not possible to say whether the current ecological view of reef fish assemblages is correct, nor what spatial scale is correct on which to base management if this view is correct."

Fish movement also may have consequences for the interpretation of results from long-term monitoring. These studies typically rely on data collected at one time of year (a "snapshot") within a limited stream reach. However, if fish movement causes enough variation within years, comparing snapshots of population abundance, species composition, community structure, and community stability among years may be misleading (Decker and Erman 1992). Major unresolved controversies in the literature on stream-fish ecology revolve around the issue of temporal variability (e.g., Grossman et al. 1982, 1985, 1990; Yant et al. 1984; Rahel et al. 1984; Matthews et al. 1988), which indicates a need to conduct studies at temporal and spatial scales that are appropriate to the animal's life history rather than those that are convenient for the investigator (Addicott et al. 1987; Wiens 1989).

The RMP also has important implications for the way stream salmonids and their habitat are managed. For example, under the RMP habitat enhancement is assumed to benefit only the population within the enhanced reach, usually by influencing in situ processes such as overwinter survival. However, as described above, our study of log drop structures showed that fish populations increase significantly not only in the treatment sections, but also in the adjacent controls, although to a lesser degree (Riley and Fausch 1995). Data reported by Hunt (1971) showed a similar phenomenon in Lawrence Creek. Thus, as a result of fish movement, habitat enhancement may provide benefits over a length of stream much longer than the improved reach. Moreover, cost–benefit analyses of habitat enhancement versus stocking, such as those performed by Hunt (1971) and Burgess and Bider (1980), may have yielded different results if population effects beyond the enhancement reach had been considered.

Special angling regulations are another technique often used in stream-fish management. To achieve the goal of producing more or larger fish, these regulations usually include restricted size and bag limits or catch-and-release regulations designed to "recycle" fish within the fishery. It is not uncommon for certain sections of a stream to be designated as catch-and-release while adjacent sections remain under normal regulations that allow anglers to keep several fish per day. Many times these regulations are successful (e.g., Anderson and Nehring 1984), but sometimes they are not (Hunt 1980). If special regulations do not work, it may be that compensatory processes replaced angling mortality with other sources of mortality (Klein 1974; Alexander 1979). However, special regulations could also be ineffective because fish periodically move outside the designated reach and are subjected to normal angling pressure. If this possibility is not considered, as would tend to happen under the RMP, designated reaches may be made too short to achieve the desired results.

Managing fish under the RMP also has implications for hatchery programs. For example, if fish are assumed to be sedentary, hatchery plants can be made within one stream section and not affect wild fish in other sections. When the hatchery fish are almost immediately removed by intense angling pressure, this is probably true (Behnke 1992). However, for streams with less angling, there is the potential for competitive interactions (Vincent 1987), genetic effects (Marnell et al. 1987; McCracken et al. 1993; Perkins et al. 1993) or other consequences as the two populations become mixed through fish movements.

The recent emphasis on watershed management is based on the idea that perturbations in upstream areas of the watershed often degrade downstream reaches. If fish movement is common, problems could also result from the fish moving to the perturbation, rather than vice versa. Upstream fish populations could thereby be affected by perturbations that originate downstream (e.g., Crisp et al. 1984; Winston et al. 1991; Osborne and Wiley 1992). For example, Meyers et al. (1992) showed that brown trout in a Wisconsin stream moved downstream to overwinter in reaches that during the summer were warmwater habitat not managed for trout. A fish manager faced with an unexplained decline in upstream fish populations, and who does not consider the possibility of fish movement, may not recognize that degradation in the downstream, "unsuitable" reaches is the problem. Similarly, our research in Colorado streams showed that hundreds of fish may move past a given location during the summer (Riley et al. 1992). Assuming that this movement is adaptive, blocking it with improper road crossings or dams could have serious consequences throughout the watershed (cf. Linfield 1985).

Recommendations

Research on the movement of resident fish in streams has been hampered because stream-fish populations are inherently difficult to sample, especially over large spatial scales. Because only relatively short reaches can be repeatedly surveyed, there is an inherent bias against the detection of longer range movements. This does not reflect a lack of effort, but rather the difficult systems in which we work. Our mistake as scientists has been a failure to fully appreciate the potential biases of extrapolating the results from short reaches to entire populations that occur at larger scales. Fortunately, there are some steps we can take to address this problem.

When designing studies of fish movement, researchers should strive to incorporate methods to permit movement to be detected over large spatial scales. This could include sampling many short study reaches throughout a stream system, or radio telemetry to track fish directly. Where possible, fish should be individually marked and the exact location of release recorded, as opposed to batch marking fish within stream reaches.

Much stream research and management involves repeated sampling of specific stream reaches, which affords the opportunity to "test" the null hypothesis of restricted movement, even if fish movement is not the point of the investigation.

If investigators can achieve high capture efficiencies so that nearly all fish in a reach are permanently marked during initial sampling, then a large number of unmarked fish captured during resampling indicates immigration. Thus, the proportion of immigrants during subsequent surveys becomes a direct measure of fish movement. For example, because we were generally able to achieve capture efficiencies >95% using three-pass electrofishing techniques in our study streams (Riley and Fausch 1992), the presence of large numbers of unmarked fish during resampling alerted us to fact that fish movement was common (Riley et al. 1992). Cunjak and Randall (1993) used similar reasoning to document the in-stream movements of young Atlantic salmon (*Salmo salar*) during winter and early spring in three Nova Scotia streams. Based on the high frequency of immigrant (unmarked) fish in their seasonal samples, and the low recapture rate of marked fish (2–30%), they concluded that "in-stream movement was extensive", even beneath ice during winter.

Another technique useful in small streams is two-way weirs (Riley et al. 1992). A single weir on a stream can be used to measure the number of fish moving upstream and downstream past a given location, and weirs spaced throughout a stream can be used to measure distances moved by individually marked fish. Using these techniques in Colorado, we have been able to monitor the movements of hundreds of trout per year per study stream. As with any method, however, one must consider potential sampling biases such as differential escapement from weirs of different design.

Additional theoretical work is needed in analysis of fish movement data. Stott (1967) proposed a method to detect sedentary and mobile fractions within a population, but its statistical properties are not well known. Bergersen and Keefe (1976) presented an index of fish movement suitable for streams, and Hilborn (1990) developed maximum-likelihood estimators to describe fish-movement patterns based on tagged recaptures. Swihart and Slade (1985) outline a test to determine if an animal's location at time $t + 1$ is independent of its location at time t. Hestbeck et al. (1991) present a method for testing whether animals tend to return to the same seasonal locations, or tend to move to new locations in successive years. To our knowledge, none of these methods has been widely applied to resident fish in streams.

Although we are beginning to understand that many stream fish do move, we have little reliable information as to the causes. Based on the studies to date, it does not appear that simple explanations involving population density (Chapman 1966; Jenkins 1969; Mense 1975; Heggenes 1988b; Hesthagen 1988) or fish size (Bachman 1982) are wholly accurate. Similarly, it is likely that the frequency of movement varies among streams. For example, movement may be more common in variable or harsh systems like the ones we study, and less common in more constant or benign ones such as spring-fed streams or large rivers. Undoubtedly, different factors affect different species and life-history stages at different times, making generalizations difficult. Laboratory studies have provided some useful information (Wilzbach 1985; Mesick 1988), but the nature of the question demands field work. A behavior that may involve movements over many tens of meters cannot be satisfactorily studied in a circular tank. The genetic basis of movement has received some attention (Raleigh 1971; Kaya 1989;Van Offelen et al. 1993), but deserves more (Northcote 1992).

There is clearly a need for new theories that explicitly address the mechanisms that cause stream salmonids to move, and field experiments to test the theories. However, because fish are extremely plastic and adaptive in almost every aspect of their biology and life history, an understanding of when and why fish move will not come easily. Fortunately, we expect the explanations to be interesting.

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